Systematic Zoology

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Basic Questions of Systematics

THOMAS BORGMEIER

THE following discussion is based on the introduction to my monograph on the neotropical army ants (1955). As is well known, revisionary studies not only broaden our factual knowledge, but also permit an amazing insight into the nature of systematic research, about which the most contradictory views are in circulation.

Systematics as a Science

Systematics or taxonomy can be defined as that branch of biological science which explores the order existing in the Plant and Animal Kingdoms and represents it by means of a system of concepts (the categories). That there is order in nature is a presupposition of any scientific research, as Caldin exhaustively demonstrated in his book *The Power and Limits of Science* (1949, p. 61). Nature is not a Chaos but a Cosmos. There is a system in nature, independent of any human consideration. The systematist seeks to reproduce this system of nature in a natural system. Order is not carried into nature, but rather it is abstracted from her. "Nature itself has her own system with regard to which the systems of the authors are only successive approximations" (Agassiz, 1869, p. 51).

As the science of order ("taxonomy"), systematics is a pure science of relations, unconcerned with time, space, or cause. Unconcerned with *time*: systematics is non-historic and essentially static; it knows only a simple juxtaposition of different conditions of form. Unconcerned with *space*: geographical factors are not primary criteria in the definition of taxonomic units. Unconcerned with *cause*: systematics has no explanatory function as far as the origin of the system is concerned; it is merely comparing, determining, and classifying. "Systematics is only directed to an apprehension and orderly arrangement of the stable elements in nature, which exist as actual facts independent of any theory or interpretation. . . . It seeks to express the order and relationships existing in the objects themselves, but does not say anything about their origin." (Schindewolf, 1950, p. 436, trans.) "Any kind of systematics is independent of the possible origin of the objects to be classified" (Kuhn, 1951, p. 155, trans.). Horn stated: "Taxonomy is ordering, without saying anything about the way in which this order has come into being." (1929*a*, p. 42.)

Systematics is a true science, because science is nothing more than demonstrable knowledge, rationalized perception. Its method is inductive, like that of all natural science. It rests on observation and intellectual penetration, on analysis and synthesis. *All* facts observed which can help the systematist to build the system are important to him. This includes even the genetic relations of the organisms, for example, the facts of sexual dimorphism and polymorphism observed in the army-ant genus *Eciton*. But the real task of the systematist begins only then, and it consists in morphological comparison; so that in the case of *Eciton*, we can talk about worker-systematics, female-systematics, and male-systematics. The systematist is therefore a biologist and a comparative morphologist at the same time. Even Linnaeus was not a mere cataloguer or "skin-zoologist" concerned only with external characters, as we read many times. If he had known all the castes of *Dorylus helvolus*, he would certainly not have described the species as *Vespa* nor would he have named separately each of the three castes.

Comparative morphology is the backbone of systematic research. Form stands

at the center of interest. The phenotypic characters observed and the conditions of similarity are not counted; they are rather, as it were, evaluated (cf. Remane, 1952, pp. 6-11). Differences in form cannot be mathematically conceived. Systematics has nothing to do with "mathematical logic" (cf. Horn, 1933, p. 132; Hennig, 1950, p. 150). Rensch (1934, p. 110) wants to extend Kant's statement that there is as much of real science in any science as there is of mathematics, to the field of taxonomy; this view must be decisively rejected. I know of no systematist exclusively preoccupied with the quantitative analysis of characters. "The mathematical machine works with unerring precision; but what we get out of it is nothing more than a rearrangement of what we put into it" (Thompson, 1937, p. 114).

The inductive method works perfectly in the field of the so-called "exact" sciences, for instance in physics. The exact sciences state their laws in quantitative form; they are necessarily mathematical. Zoology is not an exact science in this sense, but its true results are certain and absolutely binding. However, it frequently takes a long time to achieve a system that represents the true reality of nature. For instance, let us take the story of the army-ant *Eciton burchelli:* The male was described in 1842 as *Labidus* by Westwood; the soldier was made known by Mayr in 1886 under the name of *Eciton foreli;* and the female was first discovered by Wheeler in 1921. In his work the systematist for the most part has only fragments of nature on hand, therefore his results are often only an approximation to reality. "Science commonly advances by successive improvements of approximate statements" (Caldin, p. 66). Nature is highly complex and the multiplicity of forms is oppressive. Moreover, there is the subjective element which is present in any observation and evaluation of morphological relationships; this subjective element has a disturbing effect on the certainty of taxonomic concepts. The present state of research in certain groups of insects resembles chaos rather than a system. But the working method of systematics is essentially sound and is likely to deliver definite results, provided that it is properly handled.

Systematics has been contemptuously designated as only cataloguing or "pigeonholing" of specimens. Whoever thinks this, has no idea of the essence of systematic research. Just as it would not occur to a chemist to compare the study of the system of elements with the cataloguing of a librarian, and just as the discovery of a new chemical element is rightly celebrated as a scientific feat, so the investigation and classification of the elementary units of the zoological system, *i.e.,* the species, constitute a scientific study which has nothing to do with simple recording. Discovery, designation, and diagnosis of an actual new species which exists in nature as a biological unit, is equivalent to discovery of a new chemical element. It is a step forward into the *terra incognita* of nature, it is the erection of a new systematic concept which demands general recognition. For example, no sophistry can ever banish the concept *Eciton burchelli* from the annals of science. The populations corresponding to this concept may die out; but the concept remains. "Extinct species have not ceased being species, even though none still live" (de Laubenfels, 1953, p. 44).

Systematics and Phylogeny

Systematics is independent of the theory of descent. This is admitted today even by convinced evolutionists. The reasons are as follows. (1) Systematic methods provide definite results without reference to the idea of evolution; phylogenetics has no special methods, it is essentially the interpretation of systematic facts. (2) Systematics is a science; phylogeny is a hypothesis of a historical process containing a fundamentally unverifiable element (Thompson) and can therefore never be the foundation of a science. (3) Systematics is investigation of facts;

phylogenetics is often "a dangerous play with mere possibilities" (Hennig); Kant called it "a daring adventure of the mind."

Of course, any systematist is free to speculate on the probable phylogeny of certain species or genera, on the basis of systematic facts. In my "Studies of *Atta*" (1950), I myself tried to reconstruct the probable evolution of this genus, proceeding from the geographical distribution of the species and the structure of the male genitalia. But such theoretical considerations can only be evaluated as a supplement to systematics; they are without effect on true systematic research.

The widely held view that systematics must be based on phylogeny, and that to be natural the system must be a phylogenetic one, is nothing more than a relic of Darwinism. Exactly the reverse is true: phylogenetics is for the most part based on the facts of systematics. There is, therefore, no "phylogenetic systematics" but rather, as Naef has already emphasized, only a phylogenetic interpretation of systematic facts. Phylogenetics is nothing more than a "theoretical supplement to natural systematics" (Naef, 1933, p. 38). The botanist Allan wrote (1940, p. 515):

> The view that taxonomy should be based on phylogeny is very popular and is *ex cathedra* imposing. But the argument is too apt to be circular, and the 'phylogenetic' charts are generally based on taxonomic findings into which we read phylogeny, rather than deduced from any true knowledge of descent. Our phylogenies are invented to account for our taxonomic facts or theories.

And the paleontologist Schindewolf expressed himself as follows (1950, p. 461):

> Morphology and its precipitation into the natural system form the basis for the general theory of descent and the special history of evolution, but phylogeny is by no means the foundation of the system. The phylogenetic consideration only *secondarily* carries a historico-genetic, dynamic momentum into the system that already statically exists according to form and content, and tries to interpret the conceptual form-relationship as the expression of an actual blood-relationship. That is absolutely justified and even necessary, unless we are willing to relinquish an understanding of the forms. But it should be kept in mind that this is only an *interpretation of the existing system* and that no new insights have been obtained by a special phylogenetic method. [Translation.]

Walther Horn expressed similar thoughts at the Third Convention of German Entomologists in Giessen (1929*d*):

> Zoology is a science and phylogeny is a matter of belief. In our systematic studies of Recent and sub-Recent insects it is of relatively little consequence whether we are monophyleticists, polyphyleticists, or aphyleticists. The main thing is whether we recognize and make use of the systematic relationships. From the aphyletic attitude there can never result any detriment to systematic work. Its aim is simple typological biology, exactly as in the old comparative anatomy and the modern comparative physiology. [Translation.]

That very valuable systematic work can be accomplished with the aphyletic attitude is evident from the generic revision of Cynipoidea by Lewis H. Weld (1952), of which the author remarked right at the beginning: "This is not a contribution to the literature of evolution." I have worked with this difficult group myself and am persuaded that Weld's paper will be basic for a long time. If Kinsey's papers (1930, 1936) are compared with it, the following statement of Horn will be recalled (1929*d*, p. 93, trans.): "Theoretically, phylogeny is a beautiful idea, but it is often harmful by reason of the fact that on the basis of prejudiced, one-sided, and therefore insufficient preliminary studies it leads to the drawing of fantastic conclusions which seem to be well-founded, whereas in reality they only *conceal a defective systematic work*." Or, as a friend of mine put it: "Phylogeny is usually an attempt to hide poor taxonomy under a flowery mantel of respectability." Weld is a comparative morphologist; Kinsey a phylogenetic visionary. I cannot confirm the idea that his monographs have led to "basic general knowledge" as Sachtleben (1937) thought in a review. But that he had no clear systematic concepts and thereby caused great confusion, is clearly evident from Weld's work.

I shall conclude this section with the following citation from a paper by Blackwelder and Boyden (1952, p. 31):

> The grand object of classification everywhere is the same. It is to group the objects of study in accordance with their essential natures. . . . But in biology, since Darwin's *Origin of Species* appeared, biologists have substituted for this grand object that of "expressing the phylogenetic relationships" of organisms, a substitution which has introduced endless confusion into taxonomic theory and practice.

Systematics and Genetics

Systematics and genetics are two basically different disciplines of biology. Each has its own methods and its own problems. Systematics asks, "What is?"; genetics, "What will be?" Systematics works with morphological comparison, genetics with experiment. Systematics creates general concepts for constant entities; genetics makes causal analyses of modifications. Since there is only one truth, the definite results of the two sciences cannot contradict, rather they can at most complement each other.

The systematist is convinced that differences in the genotype are accompanied by visible differences in the phenotype, and that exact analysis of these differences is a positive way of expressing the multiplicity of organic forms in a system of categories. "After all, systematics cannot erect a nomenclature on the basis of genes and chromosomes. Concepts like 'dominant', 'recessive', etc., cannot be simply transferred to systematics; 'homozygote' and 'species' are two different things! Populations play an entirely different role in systematics than in genetics." (Horn, 1933, pp. 136-137, trans.)

One of the greatest dangers threatening systematics is the effort of certain geneticists to demolish the concept of species. They speak of pure lines, elementary species, biotypes, microraces, etc., and try to force the Linnean species out of its central position, so that one geneticist, the famous Johannsen, has even published the harsh opinion that the species concept, on account of its arbitrary interpretation, is only comparable to the concept of sausage, lettuce, and ink! (Horn, 1933, p. 134). The botanist Allan says (1940, p. 315): "The searching analyses of the geneticists begin to assume impressive proportions, but have revealed a great danger. Important and necessary as the delimitation of microspecies may be, we must hold fast to the broader concept of species if we are not to miss the forest by getting lost among the trees." Recently, the famous Swedish geneticist Heribert Nilsson took an energetic position against the species splitters and excessive species makers in his important work *Synthetische Artbildung* (1953).

The problem of the origin of species has not been experimentally resolved despite assertions to the contrary. Woltereck (1931, p. 300) assured

> that experimental genetics . . . did not advance beyond the pleomorphy of races and replaceable characters and it must make a halt before the problem of species formation and species descent as before a smooth wall, in spite of successes and results hitherto unheard of in biology. . . . What kind of wall is this which is raised between the results of our experiments and the problem which is supposed to be finally explained by those experiments? We seek for the mechanism of *speciation,* and find always again and in always clearer light, the phenomenon of *variation.* Why are these variants of no decisive use to us in understanding speciation? . . . Because the species are not increased and diversified variants, as we have hitherto assumed, but they are biological entities and stable elements in nature which belong to a category essentially different from that of the variants. Just as we are not able to produce a single gene-modification by way of the accumulation and intensification of phenotypical differences, we seem also incapable to produce a new constitution, a new species, a new type at any time by the increase and accumulation of additive racial characters. [Translation.]

The Nature of Systematic Categories

All systematic categories (phylum, class, order, family, genus, species) are universal concepts abstracted from the individuals. As concepts, they exist only in the mind, but we find the basis for these

concepts in nature. As the old logicians said, they are *"entia rationis cum fundamento in re."* The categories are, therefore, not concrete things, as Nägeli and Heincke asserted. No more are they purely subjective fictions with no basis in reality as others (Zimmermann, Mertens, Dürken) think. Nor is it correct to say with Mayr that the "species" are realities, but the higher categories are pure abstractions. "Only the individuals have true reality, tangible objectivity, which can be perceived by the senses. But a single individual never represents the whole species concept." (Schindewolf, 1950, p. 437, in translation.)

The nature of categories can easily be made clear if we begin with the artifacts of human workmanship. General concepts such as "chair," "table," "cupboard" are immediately comprehensible in daily life. When I speak of "chair," I do not mean this or that individual chair, but rather what is common to all chairs, the concept "chair." This concept is not an arbitrary fiction. No more is it something real in the sense that individuals are real. It is simply a general concept or an abstraction "with a basis in reality." The same applies to the group-concept "furniture," by which I can put together the "species"-concepts of "chair," "table," and "cupboard."

In nature too, there are "group-formations of different rank and extent, and those are *objective facts* which are the foundations of our categories no matter what designations they have" (Schindewolf, 1950, p. 441, trans.). The systematist can, therefore, not act purely arbitrarily like the astronomer who combines several stars in a constellation. The systematist must keep to the similarities and differences present in organisms. A few systematists may be idealists in theory, but all of them are realists in practice. The realistic-minded systematist is convinced that the essential orderliness of nature can be laid bare and can be expressed by concepts which are meant to apply, as the old logicians said *"toti et soli definito."*

Let us take the group-concept "ant." It is unimportant whether we call it "Formicidae" or "Formicoidea;" that is, whether we evaluate the group as a family or a superfamily. It is important only that this group-concept is founded in nature. Delimitation of this concept is not a matter of agreement or convenience. The extent of this concept is permanent and stable. The concept was derived from observation of nature. It would be absurd to call such an objectively well-founded concept a fiction of the human mind. What is understood by "ant" has been established for all time.—It is not to be denied that arbitrary concepts do exist in zoological nomenclature. But then, the systematist is arbitrary, not nature. In nature there is order, in nomenclature unfortunately we often find chaos.

What applies to the concept "family," also applies to the concept "genus." It is an abstraction "with a foundation in reality." Therefore it is by no means a purely subjective fiction or an "artificial creation" (Mayr, 1949, p. 491) but a natural unit. Whether a genus is large or small, whether it includes many or only a few species does not finally depend on the subjective judgment of the taxonomist. Independent of any phylogenetic speculation, the systematist must try to recognize and define unequivocally the generic groups by careful morphological comparison of species. A thousand-fold experience demonstrates the fact that there are generic groupings in nature which are separated from each other by sharp gaps. The delimitation of genera may be subject to fluctuations which depend partly upon the experience of the taxonomist, partly also on the degree of knowledge to which research has advanced in a certain group. "Concepts of genera change with the increased knowledge of individual species" (Weld, 1952, p. 345). But barriers are set up against subjective evaluation of generic characters by the facts existing in nature. These fluctuations will certainly come to a standstill when all the facts are known and have been objectively evaluated. If

this goal of a rational penetration of reality, which is the ideal in the mind of the systematist, were not attainable, no systematics would have any sense at all. Without this belief the incredible labors of taxonomists would be without hope. The difficulty of the task forms the stimulus and the motivation of systematic research.

What the investigator finds in nature is a graduated multiplicity of forms. This makes possible the erection of an hierarchic system consisting of a series of categories. These are in a definite condition of subordination. The higher categories include those of lower rank down to species. Every category represents an idea or a type, but this idea is based on facts, provided that it was "naturally" and not "artificially" formed. The systematist is therefore an idealist and a realist at the same time. Comparative morphology is both "idealistic" morphology and empirical research. But all research begins with the individual. The pure idea of form, the pure type, exists nowhere in nature. For instance, there are no ants which would present only the general characters of the family Formicidae. But

> every individual embodies the complex of characters . . . of the sum-total of hierarchic types to which it belongs. It therefore simultaneously embodies the type of its species, its genus, family, order, etc., and it is a matter of comparative and abstractive consideration to sift these type characters of varying size and extent, and to separate them from each other. [Schindewolf, 1950, p. 241, trans.]

The Species as Fundamental Unit of the System

The concept of species as "the group of individuals distinguished by an irreducible set of constant properties and connected by descent and genetic relationship" (Thompson, 1937, p. 24) forms the real fundamental unit of the system. Every animal unequivocally belongs to a certain species. All organic nature is specifically constituted; this applies both to recent and to fossil organisms. This fact is supported by so overwhelming a number of observations that it must be designated a natural law. It is also granted by convinced evolutionists.

The geneticist Bateson wrote (1894, p. 2): "The existence of specific differences is one of the characteristics of the forms of living things. This is no merely subjective conception but an objective, tangible fact . . . . So much is being said of the mutability of species that this which is *the central fact of Natural History* is almost lost sight of, but . . . this fact must be boldly faced. There is nothing to be gained by shirking or trying to forget it." Twenty years later (1913, p. 12) he expressed the same thoughts: "Specificity is a universal attribute of organized life."

Another geneticist, Dobszhansky, writes (1937, p. 306): "There is a single systematic category which, in contrast to others, withstood all the changes in the nomenclature with an amazing tenacity. That is the category of species . . . . In most animal and plant groups, except in the so-called difficult ones, the delimitation of species is subject to no dispute." And again (p. 309): "Despite all the difficulties encountered in classifying species in certain exceptional groups of organisms, biologists have continued to feel that there is something about species that makes them more definite entities than all other categories."

At the 87th Meeting of the Society of German Naturalists in Leipzig in 1922, the paleontologist Johannes Walther made the following declaration which caused no little excitement (1923, p. 153):

> When I concluded my biological training in Jena 40 years ago, in order to devote myself entirely to the study of ancient life and its geological environment, I approached the factual material with the principles which my teacher Ernst Haeckel had so spiritedly supported to the last. Fascinated by his ideas, it seemed to me an easy and successful task to follow up the series of forms gliding slowly from one to another and to prove their causal dependence on the changes in environment. But during my work I was gradually forced to give up that suggestive point of view, and with time I became firmly convinced *that the*

species were just as constant in past ages as they are at present. Just as today there are some species which vary greatly and live among numerous "good" species which do not vary at all, so has it always been. There have been greatly varying forms in every geological period, but they are just as extinct as their companions which did not mutate, and no causal historical connection whatever can be discovered between variation and species formation in the geological periods that are past. [Translation.]

Since Darwin's "Origin of Species" (1859) there has been a tendency among biologists to doubt the fundamental importance of the species and to deny its central position. The species are considered as increased varieties, but it has been forgotten that the concept "variation" has no meaning and is without content unless the specific definition has been clearly established before. Therefore Agassiz has already asked: "If there are no species, how can they vary?" And Bateson says (1893, p. 80): "The belief that living beings are plastic conglomerates of miscellaneous attributes . . . is a fancy which the study of variation does not support." In his recent work *Synthetische Artbildung* (1953, p. 252) Nilsson writes (in translation): "To Darwin evolution was a gradual problem . . . . Everything was in a continuous flux. Thus it was easy to get over the species limits. But here is the fundamental difficulty according to our experience with the structure of the species. It is unsurmountable. For the species is not made up of pan-genes which can be displaced, but rather it is composed of hereditary genes which are stable . . . . The species is constant."

What the conscientious systematist who is aware of his responsibilities discovers in nature, is not a planless flux of indefinitely plastic forms, but rather separate species which can be distinguished by a certain set of common characteristics. "Even the presence of more or less numerous mutations, races, subspecies, and the like, within the species does not alter the fact that the fluent transitions demanded by continual change are not forthcoming. The world of living and fossil organisms is not a continuum but a discontinuum" (Bertalanffy, 1949, p. 95). All species, both the monotypic and the polytypic ones, are separated from each other by sharp gaps. "It is an uncontestable fact that all species of animals and plants are separated from each other by absolute and clear-cut characters" (Godron, 1873, p. 372). Therefore, Woltereck (1931, p. 280, trans.) claims: "The old concept of the true species as a biological entity, which almost became dissolved into elementary species, biotypes, etc., must again take up the central position which it has always occupied in the mind of systematists and specialists."

Mayr (1949, p. 103) says: "It is a curious paradox that so many taxonomists still adhere to a strictly static species concept, even though they admit freely the existence of evolution." To that it can be replied that the static species concept is forced upon the systematist by the facts. We can speak of "dynamic" species only in the sense that certain species produce races or subspecies, but the formation of races is rigidly bound to the species limits and every *Rassenkreis* is only a pleomorphic species which is sharply separated from every other species. That is admitted by Mayr himself when he says of Kleinschmidt and Goldschmidt (p. 114): "They claim that all evidence for intergradation between species which was quoted in the past was actually based on cases of infraspecific variation and, in all honesty, it must be admitted that this claim is largely justified."

In the case of the polytypic species of *Eciton,* for instance *mexicanum, burchelli* and *vagans,* the specific characters in the vast area of distribution from Argentina to Mexico are absolutely constant and every individual (whether worker, female, or male) of any race of these three species out of the whole range leaves no doubt of any kind as to which of the said species it belongs. This stability is still more surprising in the world-wide distribution of some monotypic species, i.e., of species which do not form races. In the

case of the polytropical phorid flies *Diploneura cornuta* and *Megaselia scalaris,* for instance, specimens from different continents are practically identical. The same applies to *Musca domestica.* Allan had the same experience with plants (1940, p. 515): *"Capsella bursa-pastoris* Medic. travels the world over, may drop certain forms here and there, but does not change into something else." Schilder nevertheless in his *Einführung in die Biotaxonomie* (1952, p. 21) remarks (in translation): "One must be sceptical of all statements on 'world-wide' distribution of homogeneous forms. . . ." We know whence this scepticism comes: It comes from the preconceived opinion that all species with a wide geographic distribution *must* form races. The tendency to do violence to facts in order to save an idea is clearly apparent.

It has been asserted again and again that a generally valid definition of "species" has not yet been found. I hold that to be an error. There is a whole series of good definitions which take both the genetic and the morphological element into consideration. One of the best is that given by Cuvier (1829); one of the worst that of the phylogeneticist Zimmermann (1948, p. 194). The last runs as follows (in translation): "Groups of organisms which are so similar that on superficial observation they are considered to be 'of the same kind,' that is, that they can be confused, or that a large concordance of hereditary structure can be assumed." The same author considers it "a matter of convenience where the lines between species are drawn." Also according to Dürken (1924, p. 46, trans.) "the species concept is carried into nature by man. . . . There are no natural species limits." Contrary to that, on the basis of my taxonomic experience, I hold fast to the opinion that the species is a natural phenomenon and a biological unit based on objective facts. Let us take, for example, the species of *Eciton* for which all the castes are known and which can therefore be considered as clarified. There can be no doubt about their specific difference. The concepts which the systematist combines with *Eciton burchelli, quadriglume, dulcius, vagans, mexicanum, hamatum,* are fixed for all time and are absolutely binding. Arbitrary concepts can never compel general recognition. Meglitsch says rightly (1954, p. 53): "The systematist may be arbitrary, the species is not."

The "biological" species concept is not an invention of the "New Systematics." There has never been any other species concept than the biological one. Even Linnaeus knew and used it. Cuvier, a representative of "Linnaeism" defined the species (1829, p. 16, trans.): "the assemblage of individuals descended from one another or from common parents, and of those who resemble them as much as they resemble each other." *We see that the "New Systematics" is already rather old!* Therefore, it is a mistake to speak of a "revolutionary modification of the species concept" (Mayr, 1949, p. 102). Meglitsch emphasizes the same idea (1954, p. 52): "The classical systematist developed a system of classification upon the phenotypic, and especially upon the morphological, attributes, but while so doing they comprehended the species as an assemblage which is linked together genetically in some way or other . . . . The modern systematist, therefore, has not introduced a radically new element into the philosophy of systematics." Even Hennig (1950, p. 149, trans.) admits "that there has never been, up to the present time, a systematics in which typological and genetic principles were not connected together in the most intimate manner."

When I ask "What is a biological species?" I am asking for the general characteristics that differentiate the species of organisms from the species of inorganic nature (the elements, for instance). But the systematist is primarily interested in knowing what particularly applies to every species; he is asking for specificity which separates the individual species from each other. And this question can only be made to nature herself, and in no

case in which methodical observation is joined to intellectual penetration will a definite answer fail to appear. There are no taxonomic riddles relative to species limits, if these two conditions are fulfilled.

In modern literature there is much talk about "population systematics," but it is admitted that it is difficult to define the concept "population" adequately. Mayr (1949, p. 24) takes recourse to Webster's Dictionary! Homogeneous populations are at the disposal of every myrmecologist in any ant's nest. They facilitate knowledge of polymorphism, that is, of the phenotypical complex which belongs to *one* species. But it is a childish illusion to think that ants are "a group in which specific characteristics are so clearly and easily discernible," "because the myrmecologist is blessed with material which advertises its own specific characters" (Creighton, 1950, p. 12). "Population" is a taxonomically empty concept and has no meaning so long as the species to which it belongs is unknown. But the species can only be recognized by morphological comparison of several species of the same group and this comparison is always made on the individual. The individual is the "primary object of research" of the taxonomist (Remane, 1952, p. 3). Even in the examination of series, it cannot be "eliminated" as Rensch (1934, p. 15) asked, for it is self-evident that every series is composed of individuals. Also in plant taxonomy some authors are beginning to speak of "dynamic populations" and to scorn the herbarium. Rollins (1953, p. 183) laments this "tendency to deprecate specimens" and points to the fact that also the study of variation is based on individuals.

There are also numerous cases in which a single specimen shows such characteristic features that a description of it signifies a real advance in systematic research and an enrichment of the system. Some years ago, Reichensperger (1924) described a new ecitophilous genus and species in the family Histeridae, *Synetister pilosus,* from one specimen; the species was found again 24 years later but was already sufficiently well characterized in the original description. In 1948 Brown described a minute ant from New Caledonia, *Discothyrea remingtoni,* from one holotype; as shown by the accompanying illustration, the species is so characteristic that recognizing it again should present no difficulty at all. In the Ecitonini also, various species are known only from single specimens, for example, *Labidus auropubens, Neivamyremex inca, N. maxillosus, N. physognathus, N. cratensis, N. carinifrons, N. pulchellus, N. imbellis, N. planidens, N. cloosae.* I am convinced that all these forms can be immediately recognized from my descriptions and figures and that suppressing them or not describing them would have resulted in a perceptible gap in our knowledge of army ants.

The so-called "population systematist," as is well known, uses exclusively the genetic species concept and lays considerable emphasis on interbreeding and reproductive isolation. "This criterion has nothing to do with pure systematics" (Schindewolf, 1950, p. 442, trans.). The same origin and reproduction is a theoretical postulate, but not a general criterion for determination of species. Experiments of hybridization are possible only in rare cases and even the population systematist does not proceed without comparative morphology, as Mayr himself must admit (1949, p. 121). Morphological comparison is and will remain the backbone of any taxonomic research.

Geographic factors are also to be rejected as primary criteria in species systematics. Whether two species are "sympatric" or "allopatric" is completely immaterial to their differentiation. The question may be important to the theoretician on evolution, but it has only secondary interest for the systematist. "The system can only be based on what the organisms themselves are and on the characters they show. It must put us in a position to recognize and to name the forms even without knowledge of their

origin and distribution in space. We must first be able to determine the organisms, before we can establish their geographic distribution" (Schindewolf, 1950, p. 463, trans.).

It has been asserted that in difficult genera the comparative morphological method is not sufficient for segregation of the species. The botanist Rollins, Director of the Gray Herbarium at Harvard University, takes a position on this question in a very readable paper re-printed in "Systematic Zoology" (1953, pp. 180-190). He proceeds from the fact that in every genus there are species which can be readily separated. "I do not know of a single genus in which such species may not be found." Exact study of these species teaches that all of them differ by a majority of characters. *"Unus character, character nullus."* The characters recognized as valuable form the "species standard," which is "the real key to species interpretation in the whole genus," including the more difficult series. In the genus *Arabis,* Rollins obtained reliable results by this method and he added: "I believe that the method would even permit agreement as to the number of species in *Rubus* or *Crategus.*" This method is nothing other than the comparative morphological method mentioned above. It is consciously or unconsciously used by every monographer who goes thoroughly into the matter and is not satisfied with compilations. Of course, these ideas "are fairly radical deviations from the most common present-day ideas" (Rollins).

How many species shall be described? I answer: just as many as are present in nature, no more and no less. Ornithologists frequently speak of "simplification of the system" by reducing the number of species. If species which are not species are thereby eliminated, this tendency can only be welcomed. History teaches that there was no lack of such "species" in ornithology. But if some authors go so far to ridicule the description of really new species and to demand revisions or monographs in groups where is not yet the slightest possibility for revisionary work, then they hinder the freedom of research and forget that the principal task of a systematist is to make the species of nature known. It is therefore difficult to understand why Horn (1929*c*, p. 59, trans.) presented the curious opinion: "It should be clear to the systematist that the greatest possible limitation of numbers of species is a most urgent prerequisite if we few entomologists are not to lose every future orientation." I ask: where then shall the boundaries be drawn? In his monograph on the South American weevil genus *Conotrachelus,* Fiedler (1940) lists 547 species, of which 404 are described as new. Marshall, a specialist in this group, estimates that the total number of species in this genus is probably 2000! In my opinion it would be nonsense to impose on the taxonomist any limitations other than those which are imposed by nature herself. It is a matter of course that modern standards must be applied in the case of new descriptions. Scientific systematics is more than a nomenclatural affair.

Schindewolf (1950, p. 433, trans.) speaks ironically of "purely naive descriptions of single species which, without any arrangement in a larger framework, provide only rough building stones. They represent a relapse into an epoch of research that has past." I consider this exaggerated. Every description of a species demands arrangement in a system and building stones are always building stones. Schindewolf also immediately withdraws his decision in that he adds: "With that, of course, no adverse judgment shall be passed at all on pure observation and exact description. They are *indispensable* and so far as they are carefully carried out they have lasting value and greater permanence than all the glittering hypotheses which are built on them."

The problem of species formation does not belong to systematics. Taxonomy is no "ancestor-hunting" (Blackwelder), but determination and classification of the products of evolution, i.e., of the species.

And this task is so difficult that it may be doubted if we will ever get to the end of it. Mayr's book, *Systematics and the Origin of Species* therefore, is already a failure in its title.

The Subspecies (Race) as a Partial Subcategory of the Species

It has been known for a long time that certain species split into subspecies or races. Linnaeus and Fabricius commonly speak of "varieties." Kant (1775) was the first who recognized the difference between species, subspecies, and variety. Esper (1781, *De Varietatibus*) clearly defined: "Subspecies which are generally called varieties, are to be clearly separated from them. That they took their origin from species, is clearly revealed by the perfect similarity of the essential parts."

The subspecies was first introduced into zoological nomenclature by the ornithologist H. Schlegel (1844) who added a third Latin name to the name of the species (trinary nomenclature). This practice was taken up later by entomologists and is sanctioned today by the International Rules of Nomenclature. With Darwin's *Origin of Species* (1859) began a movement which can be designated as devaluation of the species. Through the fusion of the doctrine of *Formenkreis* (Kleinschmidt) and *Rassenkreis* (Rensch) with the evolution theory the cult of races came into full swing. Originally destined to cleanse the "Augean stable" (Kleinschmidt) of ornithological nomenclature, it was eagerly seized upon by the neodarwinists (Huxley, Rensch, Mayr) and proclaimed as "one of the most productive working hypotheses of taxonomy" (Mayr). All this led to an inflation of infraspecific nomenclature, which is a symptom of decline and deterioration of present-day systematics. Taxonomy is being reduced to an affair of nomenclature. Systematics becomes the science which gives a great many names to the same thing. According to Burt (1954, p. 99) 150 subspecies have been described for *Thomomys bottae* alone, and there are more to come! Wilson and Brown (1953, p. 102) characterize the situation with the following remark: "From our experience in the literature we are convinced that the subspecies concept is the most critical and disorderly area of modern systematic theory."

Because of the abuse of "subspecies" in zoological nomenclature some authors "wish to abolish trinominalism root and branch" (Huxley). With that, there would be an end to "the tyranny of subspecific names." Such a panacea might be considered a successful solution in the case of many so-called "races" mentioned in the literature, for instance, those of *Passer domesticus* and *Phasianus colchicus* in Kleinschmidt (1926), or those of *Cyclophorus perdix* in Rensch (1934), or those of *Mimegralla albimana* in Hennig (1950, p. 136). But things are not so simple if we look a little deeper into the matter and consult nature, instead of literature. "Study nature, not books," Agassiz used to say.

If we want to find out whether actual "subspecies" do exist in nature, we must proceed from the species. Only in well worked genera whose species are sufficiently known can the study of infraspecific variation be undertaken with any prospect of success. Now experience teaches that some species have a tendency to form races, others not. "The multiplicity of races of natural as well as of cultivated species is extraordinarily different. Without perceptible reason, we see that some species break up into a vast number of hereditary races (for instance, *Daphnia longispina*), while closely related species (*Daphnia pulex*) do not" (Woltereck, 1931, p. 290). The same observation can be made in ants. We find monotypic species together with polytypic ones, sometimes in the same genus. *Eciton hamatum* is constant, *E. vagans* and *burchelli* split up into races. Wheeler (1936, p. 176) writes of *Termitopone commutata*: "The stability of the ant is attested by the fact that, so far as known, it exhibits neither

subspecies nor varieties in any part of its range." In his revision of the Dacetini, Brown found no races at all. With regard to the Diptera, Rensch (1947, p. 51, trans.), remarks: "It is striking that in this Order of insects geographic variation has hitherto been observed only sporadically." In phorid flies I never saw any race; even such wide-spread species as *Diploneura cornuta* and *Megaselia scalaris* are absolutely constant throughout their range.

Since all infraspecific variation is bound by the species limits, it is absurd to conclude that the polytypic species represents a special "collective category," in addition to the monotypic species. The Linnean species has not perhaps been "broadened" to include both kinds; it has embraced the non-dimensional and the multi-dimensional species from the beginning. The monomorphic species characters are constant in both. That a "tremendous clarification of the system" has been obtained by the distinction between monotypic and polytypic species, as Mayr, Linsley, and Usinger say (1935, p. 26), is an empty assertion. It could be said on the contrary, that the true species concept was destroyed, and the basis of all systematics was undermined. This danger was clearly seen by the botanist Wettstein who remarks "that the *Rassenkreis* of Rensch which goes beyond the species and means the establishment of a further systematic category beside the species, is a formal impossibility. General acceptance of this concept would bring chaos into systematics and would cause its collapse" (in Hennig, 1950, p. 83). Rothschild and Jordan (1906) called the *Formenkreis* "a kind of half-caste between species and subgenus." Plate writes (1914, p. 134, trans.): "The concept *Formenkreis* is superfluous if taken in the strict sense of the word, for it designates only the sum-total of all geographic variants of the species."

The basic fault of the *Formenkreis*-theory is the fact that it does not proceed from the species. Kleinschmidt writes (1926, p. 28, trans.): "The designation 'species' is ambiguous. . . . Therefore we cannot take the definition of the species as a starting point. . . . The species is a fiction of the human mind, by which a number of similar individuals are grouped together. The *Formenkreis* [form-cycle], on the contrary, is a natural unit. . . ." Some pages later (p. 33) Kleinschmidt seems to have forgotten that the species is "a fiction of the human mind," for then he declares the *Formenkreis* to be identical with the species of systematics. It should be clear that no "doctrine" can be erected on such feeble logic. The species is and remains the fundamental unit of the system, from which all research of infraspecific variation must begin.

Goldschmidt's investigations on *Lymantria* (1934) have proved that the *Rassenkreise* do not merge into each other and that races are not incipient species. In the Ecitonini I have reached the same conclusion. All the races of *Eciton burchelli*, for instance, remain strictly within the specific limits of *burchelli*, as do also the races of *vagans*, etc. There is no intergradation of any kind between races of different species, and in no case it is doubtful to which species a given race belongs. I conclude from that:

> Race and species are not equivalent categories. Species are essentially different. Races are essentially alike, because they agree in all basic structures and are linked together genetically; they differ only gradually by accidental characters or slight hereditary modifications of basic characters. The race depends upon a splitting up of the species, it represents an "epiphenomenon" of the species (Kuhn). Therefore it is nonsense to ask whether an individual "still" represents a race or "already" represents a species. There is no living or fossil animal which does not belong to a given species. The species is primary, the race secondary. Every race shows the "facies" of the species from which it has been split off. By "facies of the species" I mean the complex of specific characters which are common to all races of the same species. This "facies" is always recognizable if the species of the genus concerned are accurately compared, in which comparison, of course, all the castes must be considered. All true species, though in some cases at first glance extremely similar, prove to be sharply separated by a bridge-

less gap, provided we do not proceed from one individual but rather take the whole complex of phenotypic characters into consideration. [Borgmeier, 1955, in translation.]

Both Rensch and Mayr admit that there are no transitions between different species or *Rassenkreise*. The contradiction lying in the fact that nevertheless "border-line cases between race and species" are constantly being mentioned, is so much the more remarkable. At most, border-line cases between races of the same species could be mentioned. Since the races of one species form a reproductive community, intergradations are able to occur. The races of *Eciton* that I investigated, both the allopatric and the partially sympatric ones, could be easily separated morphologically for the most part. Rensch (1947, p. 53, trans.) speaks of the "appearance of countless intermediate stages in each grade between races and species, and between weakly and sharply differentiated species." These alleged intergradations are a plain invention to rescue an idea, namely the idea of formation of species from races.

In my opinion it is wrong to say: "There is therefore no primary morphological difference between races and species, that is, the geographic races can be considered different far-advanced preliminary stages of the species" (Rensch, 1929, trans.). Here "race" is again being taken as an independent category, while each race clearly belongs to a definite species and all the members of a *Rassenkreis* distinctly differ specifically from those of any other. That morphological criteria are used both in separation of species and in discrimination of races, does not prove that the two categories are equivalent. Morphological characters are also used in the definition of genera, but no one claims that there is no difference between genus and species. Both species and race are universal concepts applied to biological units, but the racial characters already presuppose the specific characters and are, as it were, superimposed on them. Consequently there is indeed a *primary difference* between species characters and race characters, and the fact that the specific characters are retained in every formation of a race is clear evidence for the formation of races from species, but not of species from races. "Race-formation . . . [proceeds] from above downwards, but not, as the traditional theory of descent wants to have it, from below upwards . . ." (Conrad-Martius, 1949, p. 252, trans.). "Subspecies are actually, therefore, neither incipient species nor models for the origin of species. They are more or less diversified blind alleys within the species" (Goldschmidt, 1940). Schindewolf remarks on this (1950, p. 407, trans.): "From my personal experience I can only add that Goldschmidt's deductions completely satisfy the requirements that the fossil material seems to me to impose and that he is the first geneticist to present a comprehensive explanation which does justice to the real-historical, phylogenetical findings." Arcangeli, an Italian expert on Crustacea, writes (1951, p. 77, trans.): "The opinion has been expressed by many biologists that the subspecies into which a species can be eventually divided may represent new species in process of formation. . . . Truly this is an admission which, however suggestive it may be, is not supported by any evidence. On the contrary, it is a fact that in some cases there are circumstances that are opposed to precisely the same admission." In order to illustrate the "fixity of subspecies," Arcangeli cites cases from the genus *Tylos* Latr.

Conrad-Martius points out another contradiction in the *Rassenkreis*-theory to which generally no attention is paid.

While on the one hand they try to demonstrate the impossibility of separating species and races definitely and basically by the fact that frequently closely related species are much more similar to each other than the different races of one and the same species; on the other hand, the origin of the species *out of* the race is explained by the fact that the races must have removed themselves far enough from each other in their characters. According to this, different species would be expected to be separated by a sharper gap

than the races of one and the same species [1949, p. 258, trans.].

In all attempts to define the nature of the subspecies, geographic replacement plays a great role. Rensch (1934, p. 14) speaks of the "primacy of geographic distribution," but if we examine his statements more closely it will be seen that he is continuously working with morphological comparison. We find the same contradiction in Schilder (1952, p. 11), who wants to put "the mostly more precise criterion of distribution in space and time in the place of uncertain morphological differentiation." In spite of this affirmation, Schilder, too, always works with morphological methods. This contradiction between theory and practice is one of the best proofs of the primacy of form and the fundamental significance of morphology. No systematics can be erected on locality labels. Systematic research is unthinkable without comparative morphology.

From my experience with *Eciton* I am convinced that the subspecies can be purely morphologically conceived. But its recognition is more difficult than that of the species, because the differences are usually finer. The method for recognition of subspecies is about the same as that recommended by Rollins for the study of species. After the determination of the species we proceed from cases in which the racial differences are clearly evident, for instance, in the case of *Eciton vagans* from the subspecies *angustatum* and *mutatum* of which all castes are known. These then form the "standard" for recognition of the other races of the same species. Lack of material of sexual forms from the whole range of distribution often renders the results uncertain. Systematics is a science that grows by trial and error. Also exact determination of the nominal race is important. But most important is the comparative evaluation of the *individual* phenotypic characters which is the basis of systematic research. Such racial characters may be different in subspecies of the same species: proportion of body parts, pubescence, coloring, etc.; nature does not follow a rigid scheme. In any case, only characters which are relatively constant and discontinuous come into question for separation of races. Bogert (1954, p. 112) very rightly says: "Subspecies should be recognized only when sharp discontinuities in the trends of one or more individual characters can be demonstrated." And Ferris remarks (1928, p. 57): "These forms should not be named if the characters upon which they rest are not perpetuated from generation to generation." Individual variation and grading variation (Huxley's cline) are taxonomically worthless and do not deserve denomination.

The geographic distribution of a given race can be determined only after the establishment of the morphological difference. As is to be expected, every race inhabits a partial zone of the total area of distribution of the species. In contrast to species, the subspecies is geographically definable, but geographic isolation is rather a condition of morphological differentiation, not its cause. Subspecies can originate abruptly by mutation in any place within the range of the species. The primary factors of race-formation seem to be endogenous; exogenous factors have at most an auxiliary function. The race, therefore, is not a type of adaptation to the landscape as is frequently asserted. No racial character of *Eciton* has any adaptive significance.

According to Mayr the subspecies is a purely subjective concept. According to Brown and Wilson it is a "typological relic," and they add (1954, p. 176): "The experience of the past year has strengthened our opinion that any particular subspecies pattern is determined arbitrarily by the individual taxonomist's choice of characters, and any trinomen employed is fitted uncomfortably to a minority of the geographic variable characters." It must be admitted that many "subspecies" (perhaps most of those mentioned in the literature) are " authors' subspecies." It may even be that I have myself erred in the

evaluation of subspecific characters in some cases in *Eciton*. But I am firmly convinced that there are true subspecies in nature, that the subspecies is justified as a partial subcategory of the species, that it is a biological unit existing as an objective reality independent of man's contemplation which forms the basis for the concept "subspecies" (or "race"). I am further convinced that careful morphological comparison will lead to certain recognition of such concrete entities and that, for example, no competent taxonomist will succeed in demonstrating that *angustatum* and *mutatum* are not valid subspecies of *Eciton vagans*. The distinctive characters were not selected arbitrarily, they were derived from nature. To call the two forms "species" would be quite illogical, as long as comparative morphology is considered as the basis of systematic research.

In summary, I am defining the subspecies or race as a relatively constant, discontinuous variant of the species. Since not all species form races, this is not a universal category of fundamental significance, but rather a partial subcategory of species. The systematist should by no means neglect the study of subspecies, nor should he regard it his primary task. The first aim of all taxonomic research is the determination and definition of species as the fundamental units of the system.

Conclusion

I am convinced, with Blackwelder and Boyden, that the introduction of evolutionary concepts into systematics has produced great confusion. The systematist may not be anti-evolutionary, but in practice he is non-evolutionary.

> No matter how convinced an evolutionist may be in theory, no naturalist and, more specially, no biologist, can work and think in that way. The systematic zoologist may assert that he is a thorough-going evolutionist, but as soon as he sits down at his table to work with his specimens, he begins at once to sort things into categories, to define and limit, and, as he does so, is perfectly satisfied that he is in contact with reality and that the method he adopts, suffices to make reality known. In other words, although he may do his best to believe in his evolutionary metaphysics, he cannot live it. He cannot think without logic nor define without concepts; and if he is to retain any belief in his work and in the validity of his science he must, in point of fact, proceed on the assumption that something corresponding to his concepts actually exist in Nature—that through them he attains a true knowledge of reality. To put the point in another way, he is forced in practice to admit that there is fixity in Nature, that a variety of different and distinct things actually exists. The zoologist may affirm, and sometimes does affirm, his complete disbelief in the reality of species, but it is in the definition of these alleged unrealities that he spends his working life [Thompson, 1937, p. 194].

Therefore, in opposition to Mayr's assertion (1949, p. 23) that 90 percent of modern taxonomic work consists in the study of variation, I venture to say that 100 percent of systematic research consists in the investigation of the stable elements in Nature. The principle task of the systematist is not "that of detecting evolution at work" (Huxley), but is the study of the work of evolution.

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T. BORGMEIER, Rio de Janeiro, Brazil, Estr. Rio Grande 2116; specialist in ants and myrmecophilous insects; for twenty years editor of the international journal *Revista de Entomologia* (22 vols., 1931–1951), and currently editor of *Studia Entomologica.*

Evolutionary Developments in Leafhoppers

(Concluded from p. 97)

knows the genera and species well enough to make the necessary observations if it is not the systematist?

Acknowledgments

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HERBERT H. ROSS is Head of the Section of Faunistic Surveys and Insect Identification, Illinois Natural History Survey, Urbana, and Professor of Entomology, University of Illinois.

Problems in the Phylogeny of the Salientia

This symposium was held at the annual meeting of the American Society of Ichthyologists and Herpetologists, in San Francisco, June, 1955. It was co-sponsored by the Pacific Section of the Society of Systematic Zoology. The chairman of this symposium, at which seven papers were presented, was Dr. G. S. Myers. The papers printed here are by BRATTSTROM, JAMESON *and* ORTON.

The Phylogeny of the Salientia Based on Skeletal Morphology

BAYARD H. BRATTSTROM

VERY little work has been done on the comparative anatomy of the skeleton of frogs and toads since Noble's summary (1922). Several osteological descriptions of species (e.g., *Leiopelma,* Stephenson, 1951) or groups (e.g., *Pseudis,* Savage and Carvalho, 1953; Microhylidae, Carvalho, 1954) have appeared. There have been no renewed attempts at the comparative osteology of an entire family or genus, though some may be in the offering (Sanders, 1953).

There have been, however, a series of important fossil finds including those of Piveteau (1937) on *Protobatrachus* from the Triassic of Madagascar and Watson's discussion (1940) of "The Origin of Frogs," (see Fig. 1). In addition, several workers have been interested in Cenozoic frogs and toads and identifications of salientians from several fossil localities have recently appeared (Tihen, 1954; Taylor, 1936, 1938, 1941*a*, 1941*b*, 1942; Zweifel, 1953; Schaeffer, 1949; Brattstrom, 1953*a*, 1953*b*, 1954, 1955*a*, 1955*b*). Most of these are concerned with Pliocene and Pleistocene salientians and are usually referable to living species or genera. Their contribution to the understanding of salientian phylogeny is not great, save for their implications to the past distribution of the various groups.

Though the fossil discoveries do not contribute greatly to the knowledge of the phylogeny of the Salientia, and though there is a dearth of data on the comparative osteology of frogs and toads, a review of salientian classification at this time might be useful in stimulating others to attack the problem of the phylogeny of the Salientia.

Osteological Characters Used for Determining Relationships

The basic need in salientian osteology is the establishment of criteria or characters

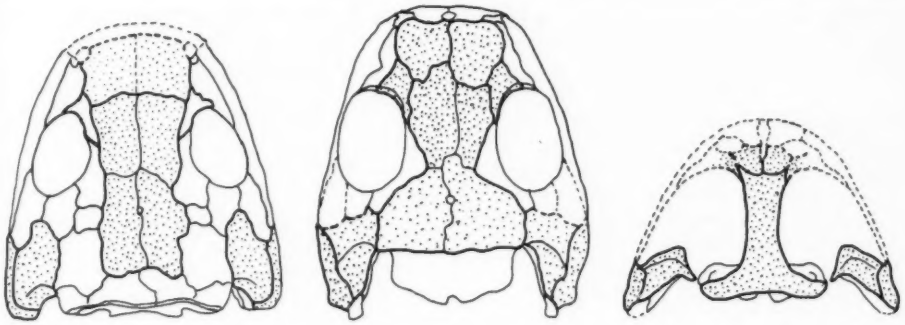

FIG. 1. Dorsal views of the skulls of: *A, Eugyrinus; B, Miobatrachus;* and *C. Protobatrachus.* All are reduced to the same size for comparison. The dermal bones which remain in *Protobatrachus* (parietal, frontal, nasal, prefrontal, squamosal, and quadrato-jugal) are stippled. (After Watson, 1940.)

that are not intraspecifically variable to be used in determining relationships. The similarity in body shape and form of most frogs and toads, in addition to the independent radiation and convergence of the many lines of salientian evolution, makes the evaluation of the characters used a most important aspect of any future study. The characters used at present are noted below.

Teeth: Noble (1922) has shown that the presence or absence of teeth in the various groups of frogs and toads is not a useful character in the determination of relationships because the several phylogenetic lines of frog evolution seem independently to have reduced or lost teeth.

Sacral vertebrae: The characters of the sacral vertebrae in salientians do not appear to be useful criteria for determining relationships due to their variability within a single species or genus (Taylor, 1942; Tihen, 1954). A detailed study of the intraspecific variation has not been given for any of the osteological criteria discussed here. A study of this kind would be needed for a true understanding of the value of any of these characters in determining relationships.

Skull: The skulls of salientians are very similar, yet there are small differences between species (e.g., the skull differences in *Scaphiopus,* Stebbins, 1951; Zweifel, 1956). These differences—when looked for in other groups—may be useful in determining specific and generic relationships, but will probably not contribute greatly to our knowledge of the relationships of the various families until all the genera of salientians are known osteologically.

Pectoral girdle: The condition of the pectoral girdle—whether it be of the more primitive, overlapping, arciferal type or the more advanced, firmisternal type—appears to be a useful character for determining some family relationships. It is evident (Noble, 1922) that the firmisternal type of girdle has developed at least twice in salientian evolution and that in some groups of frogs both types occur in the same family.

In fossil frogs the condition of the girdle is usually indeterminate because of the lack of preservation of these parts.

Vertebrae: The condition of the centrum of the vertebrae (amphicoelous, opisthocoelous, anomocoelous, procoelous, or diplasicoelous) is probably one of the better characters for the determination of family relationships. The last three types mentioned, however, may not be natural units.

Classification of the Salientia

The following partly annotated classification of the salientians indicates the

position of the several taxa as based on the comparative osteology and available fossils. The living genera are not listed for most of the families, but the genera known as fossils are included.

The taxa (families or subfamilies) related to the Leptodactylidae are so little known osteologically that, to this writer, their true position or rank seems indeterminate at this time.

Order EOANURA

Amphibamidae (=Miobatrachidae): Clearly evolved from Labyrinthodont amphibians. The changes in the skull (Fig. 1) and vertebrae are already in a salientian direction. The gross habitus is, however, salamander-like.

Amphibamus: Pennsylvanian, North America.

Miobatrachus: Pennsylvanian, North America.

Order PROANURA

Protobatrachidae: More anuran-like than the above. An elongate ilium is present, but no urostyle. The skull (Fig. 1.) is very frog-like. Vertebrae amphicoelous, free ribs present, caudal vertebrae present, presacral vertebrae 16, pectoral girdle type uncertain, probably arciferal.

Protobatrachus: Triassic, Madagascar.

Order SALIENTIA

Suborder Amphicoela

Montsechobatrachidae: Known from fragments and impressions, so this may not be a natural unit, but it does show that the Amphicoela were world-wide in distribution in the Upper Jurassic.

Eobatrachus: Upper Jurassic, North America.

Montsechobatrachus: Upper Jurassic, Spain.

Stremmia: Upper Jurassic, East Africa.

Ascaphidae:

Leiopelma: Recent, New Zealand.

Ascaphus: Recent, Northwestern North America.

Suborder Opisthocoela

Discoglossidae:

Prodiscoglossus: Upper Oligocene, France.

Discoglossus: Lower Miocene, France; Middle Miocene, Germany; Recent, Europe and North Africa.

Alytes: Lower Miocene, France; Middle Miocene, Germany; Recent, Europe.

Bombina: Miocene, Europe; Recent, Eurasia.

Pelophilus: Upper Miocene, Germany.

Latonia: Upper Miocene, Germany.

Barbourula: Recent, Philippines.

Pipidae: This group suggests a Mesozoic dispersal from some Holarctic center with a protopipa-like form reaching South America prior to the break in the Panama land bridge.

Eoxenopoides: Probably of this family; Lower Teritary, South Africa.

Xenopus: Miocene to Recent, Africa.

Pipa: Recent, South America.

Rhinophrynidae

Suborder Anomocoela: Apparently evolved from primitive discoglossids by fusion of the intervertebral cartilages resulting in a procoelous condition. Both families have had a Holarctic distribution and did not enter South America.

Pelobatidae:

Macropelobates: Oligocene, Mongolia.

Eopelobates: Miocene, Germany; Oligocene, North America.

Pelobates: Miocene to Recent, Europe.

Scaphiopus: Pliocene to Recent, North America.

Neoscaphiopus: Upper Pliocene, North America.

Pelodytidae:

Propelodytes: Middle Eocene, Germany.

Miopelodytes: Middle Miocene, Nevada.
Pelodytes: Recent, Europe.
Suborder Procoela
Palaeobatrachidae:
Palaeobatrachus: Miocene, Europe.
Protopelobates: Miocene, Europe.
Leptodactylidae (Leptodactylinae, Pseudinae, Dendrobatinae, Rhinodermatinae, Centroleninae, Heleophrynae, Cycloraninae, Myobatrachinae, Atelopodinae):
Indobatrachus: Eocene, India.
Eophractus: Eocene, South America.
Calyptocephalella: Eocene, South America.
Eupsophus: Eocene, South America.
Neoprocoela: Eocene, South America.
Teracophrys: Upper Oligocene, South America.
Ceratophrys: Upper Pliocene to Recent, South America.
Bufonidae:
Bufo: Oligocene to Recent, Europe; Pliocene to Recent, North America; Pleistocene to Recent, Asia; Recent, Africa, South America.
Diplopelturus: Pliocene, Europe.
Pliobatrachus: Pliocene, Europe.
Platosphus: Pleistocene, Europe.
Hylidae:
Hyla: Miocene (?*Lithobatrachus*) to Recent, Europe; Recent, Cosmopolitan.
Amphignathodon: Late Oligocene and Early Miocene, France; Recent, South America.
Suborder Diplasiocoela: Probably derived from the Procoela.

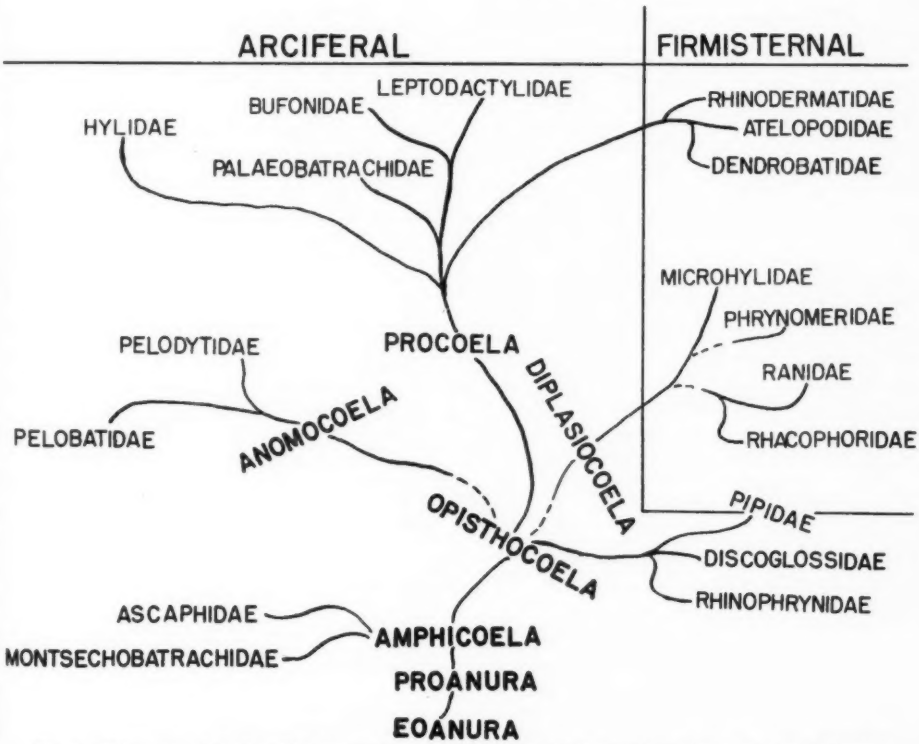

FIG. 2. Diagram showing the suggested relationships of the various taxa of the Salientia.

Ranidae:
Rana: Miocene to Recent, Asia, Europe; Pliocene to Recent, North America; Recent, Africa, Australia, South America.
Ranavus: Miocene, Europe.
Aspherion: Miocene, Europe.
Rhacophoridae (Polypedatidae)
Microhylidae
Phrynomeridae

Conclusions

The relationships of the salientian families and groups as based on the available osteology and fossils is suggested in Figure 2. This figure is not designed to be a true phylogenetic tree, but a diagram indicating the suggested relationships of each of the taxa.

It is felt that the phylogenetic position of the Eoanura, Proanura, Amphicoela, and Opisthocoela are relatively accurate and that they are all primitive groups. The true relationships of the other taxa are not well known. This is largely due to convergence of characters in the various taxa which have undergone independent but similar radiations.

It is apparent that more osteological studies of frogs and toads are needed on a generic and family basis, and on a world-wide scale. This is a large undertaking, but it is probably the only way an accurate estimate of the relationships of the various taxa will be achieved.

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BAYARD H. BRATTSTROM, Department of Biology, Adelphi College, Garden City, N.Y.

Life History and Phylogeny in the Salientians

DAVID L. JAMESON

THE life history of various plants and animals frequently offer considerable assistance in determining the phylogenetic positions of the members of a group of related species. Courtship patterns, for instance, have helped in the determination of phylogenetic relations in salamanders (Noble, 1925*a*) where these patterns show a rather clear-cut sequence which appears to follow the morphological phylogenetic steps.

One type of phylogenetic tendency that may be found in animals occurs when several different morphological groups appear to have evolved independently along parallel lines. Some of the difficulties in the interpretation of the phylogeny of the frogs and toads are the result of parallelism and convergence exhibited by both morphological and life-history characteristics. Several aspects of the general subject of amphibian life history have been reviewed previously by Sampson (1900, breeding and development), Noble (1925*b*, 1927, life history), Lutz (1947, 1948, development) and Jameson (1955, courtship and mating behavior).

This discussion is intended to demonstrate selected aspects of the variation and parallelism shown in salientian life history and to emphasize that these occur in independent phylogenetic lines. Four parallel tendencies appear in the life history of the salientians: (1) the increasing role of the female in courtship, (2) the opposition of the cloacas during oviposition, (3) the transfer of much or all of the courtship and spawning behavior from the aquatic to terrestrial situations, (4) the increasing care of the eggs.

The more primitive breeding condition may be that found in the purely aquatic breeders such as *Bombina* (Liu, 1950), *Xenopus* (Bles, 1905), *Rhinophrynus* (Stuart, 1935), *Scaphiopus* (Bragg, 1944, 1945), *Bufo* (Aronson, 1944) and most *Rana* (Noble and Aronson, 1942). In these the male calls, thus attracting the female to the breeding site. The calls serve a very important role in the courtship of most frogs and toads, both in spacing out the males (Martof, 1953) and in attracting the females. The male *Ascaphus* (Noble and Putnam, 1931), lacking a voice, is forced to seek out the passive female. Males of some *Scaphiopus* will pursue the female as soon as she is sighted, while males of other *Scaphiopus*, *Scutiger* (Liu, 1950), *Bufo*, *Rana*, *Rhacophorus* (Liu, 1950) and *Syrrhophus* (Jameson, 1954) call until the female approaches rather near, and then pursue her to achieve amplexus. During the approach or pursuit of the female several frogs have special calls, and *Syrrhophus*, a terrestrial breeder stimulates the female by the use of his hind legs. Males of *Microhyla* (Jameson, 1955) and some *Scaphiopus* and *Hyla* (Smith, 1940) will call until touched by the female, while males of other *Hyla* must be almost attacked by the female before amplexus (Noble and Noble, 1923). In *Dendrobates* the females pursue the actively moving, calling, male (Dunn, 1941). Thus we can trace an increasing role of the female in the courtship pattern which may have phyletic significance.

Most of the frogs that are generally considered primitive (*Bombina*, *Rhinophrynus*, *Xenopus*, *Scaphiopus* and *Scutiger*) have amplexus in the pelvic regions but *Ascaphus*, *Alytes* (De L'Isle de Dreneuf, 1876) and *Pipa* (Bartlett, 1896) have modified their amplexus to adjust for specialized types of oviposition and care of the eggs. *Ascaphus* has an intromittent organ that assists in fertilization

TABLE I—SELECTED EXAMPLES OF SALIENTIAN LIFE HISTORIES

	AQUATIC DEVELOPMENT				DIRECT DEVELOPMENT	
	WITHOUT NESTS	AQUATIC NESTS	TERRESTRIAL NESTS	TADPOLES CARRIED TO WATER	TERRESTRIAL NESTS	EMBRYO CARRIED UNTIL BIRTH
ASCAPHIDAE	*Ascaphus*				*Leiopelma*	
DISCOGLOSSIDAE	*Bombina*			*Alytes*		
	Xenopus			*Pipa*		*Pipa*
RHINOPHRINIDAE	*Rhinophrynus*					
PELOBATIDAE	*Scaphiopus*					
	Scutiger					*Gastrotheca*
HYLIDAE	*Hyla*	*Hyla*	*Phyllomedusa*	*Hemiphractus*		*Nectophrynoides*
BUFONIDAE	*Bufo*					*Rhinoderma*
ATELOPODIDAE				*Dendrobates*		
DENDROBATIDAE				*Phyllobates*		
LEPTODACTYLIDAE	*Helophryne*	*Leptodactylus*	*Zachaenus*		*Eleutherodactylus*	
RANIDAE	*Rana*	*Rana*			*Syrrhophus*	
	Staurois				*Rana*	
RHACOPHORIDAE		*Rhacophorus*				
MICROHYLIDAE	*Microhyla*				*Oreophryne*	

of the eggs. *Alytes* utilizes a cranial amplexus as an aid to fertilization, deposition, and attachment of the eggs to the hind legs of the male. A very complex mating process has been developed in *Pipa* in adjustment to the ovipositor and the dorsal brood pouches of the female. The several "higher families" have pectoral amplexus which serves to bring the cloacas together during mating. Various complex and more or less reflex movements occur in these frogs during coupling which allow the opposition of the cloacas at the instant of oviposition. In *Bufo* only the female flexes during amplexus, while in *Hyla* the female flexes first followed by the flexure of the male. *Microhyla, Rana, Staurois* and *Rhacophorus* males flex first, followed by flexure in the female. The deposition of the eggs into a triangular area formed by the legs serves to emphasize the relationship between *Rana and Staurois*. The occurrence of cloacal opposition in these "higher families" may be of phylogenetic significance, since the amplexus of *Ascaphus, Alytes* and *Pipa* are obviously specialized conditions.

Most amphibians mate and spawn in aquatic situations, but in *Scutiger, Staurois,* and some *Hyla* and *Microhyla* courtship and coupling are terrestrial activities, the mated pair moving to water to spawn. *Rhacophorus* and *Phyllomedusa* (Lutz, 1947) mate and spawn in terrestrial situations, depending on rain to transport the tadpoles to the proper places for future development. *Alytes, Dendrobates* and some *Hylidae* mate and spawn in terrestrial situations, the males later carrying the tadpoles to water. Embryos of at least some species of *Leptodactylus* (Mulaik, 1937) and *Syrrhophus*, and those of *Rana opisthodon* (Boulenger, 1886) develop entirely within the nest. Embryos of *Leiopelma* and *Eleutherodactylus* also develop in a terrestrial nest and one or the other of the parents remain near the nest during development. A few *Gastrotheca* and *Pipa, Nectophrynoides* (Orton, 1949), and *Rhinoderma* (Sampson,

1900) have modified life histories each carrying the developing embryos until they hatch as fully developed frogs. In *Pipa* the female has dorsal brood pouches, the *Rhinoderma* male utilizes the enlarged gular pouch, and *Nectophrynoides* is ovoviviparous. The method of mating in *Rhinoderma* and *Nectophrynoides* is unknown. *Pipa* may have developed brood pouches in a terrestrial situation and subsequently returned to a completely aquatic life history. The transfer of courtship from aquatic to terrestrial situations is more than likely related to the care of the eggs during development.

The majority of amphibians have aquatic development and most tadpoles are rather generalized for pond life. A large number of frogs and toads have specialized life histories which provide for protection and care of the eggs as shown by a few examples in Table I. Members of several families build aquatic nests (dams etc.) which protect the developing eggs from aquatic insects. Others build terrestrial or aboreal nests where later rains will transport the tadpoles to ponds or streams for the completion of their development. Several families have species which carry the eggs until they hatch as tadpoles.

Orton (1949) has pointed out that at least some member of ten of the thirteen families given in Table I has direct development, the eggs hatching as fully formed frogs. Some of these use nests, and others carry the embryo until hatching. Lutz (1947, 1948) feels that there is a definite tendency in salientians toward direct development.

Of immediate value may be the use of life-history data in determining species affinities. The minor differences between the several related species of *Rana*, or of *Bufo*, or of *Scaphiopus* are not important in the study of overall evolutionary trends, but they are quite likely important in serving as isolating mechanisms maintaining species specificity where the ranges of closely related species overlap.

Except for the type of amplexus, which only partly and tentatively may be used to relate the "primitive families" as separate from the "more advanced" families, the life-history characters appear at random throughout many families. In fact closely related species or genera are frequently quite different in their habits. Males of some *Scaphiopus* pursue the female on sight, some wait for her approach, and others wait till shes touches. Some *Rana*, *Gastrotheca*, *Hyla* and *Leptodactylus* have direct development, while others have aquatic tadpoles. Some *Hyla* mate and spawn in water, some in trees, and some on the ground. Much of this parallelism appears to be interrelated and directly correlated to the morphological tendency toward direct development and to occur independent of phyletic lines. As such the use of life history data in determining over-all phylogeny in the salientians is limited.

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D. L. JAMESON is Assistant Professor of Zoology, San Diego State College, San Diego, Calif. The writer wishes to thank G. L. Orton and B. Brattstrom for reading the manuscript.

The Bearing of Larval Evolution on Some Problems in Frog Classification

GRACE L. ORTON

THE extreme specialization of the frogs (Order Salientia) and their poor early fossil record hamper our efforts to discern the principal evolutionary lines in this relatively small but seemingly inscrutable taxonomic group. From the nature and limitations of the data that have accumulated, interpretations of frog phylogeny are unavoidably conjectural, and understanding perhaps depends as heavily on one's ability to use concepts of systematics and evolution theory in general as it does on the direct evidence from the frogs. Classifications based on various combinations of external characters, on certain features of the skeleton and musculature, etc., have helped to clarify many problems, but none of the classifications proposed in the literature thus far are adequate by the exacting standards of modern systematics. It is increasingly apparent that major progress in frog systematics will require both more extensive and more closely integrated studies than have been customary in the past. The basic comparative anatomy and developmental morphology of the frogs need very thorough investigation, on a much broader scale than has yet been attempted. Developmental characters, in particular, are still commonly underrated and neglected as materials for the study of frog systematics, though they offer very rewarding clues to evolutionary trends and taxonomic understanding.

The present paper discusses some general aspects of larval evolution in the frogs, and some problems in the use of larval characters to help designate the more primitive families and to interpret their relationships, together with brief comments on some analogous problems in the fishes which may contribute indirectly toward a better understanding of larval evolution in the frogs. The presentation is deliberately speculative, in the hope that the disagreement thus invited may help to stimulate some of the needed studies.

It should be pointed out that I apply the term "tadpole" only to the larva of the frogs, in contrast to the less restricted and sometimes misleading use of the term by some authors to designate various unrelated chordate larvae which are very different from the frog larva in their morphology and their evolutionary background.

Geological History

The rich variety of adaptive specializations and structural peculiarities which tadpoles display can easily divert our attention from the long time gap in the early geological history of the frogs from which we have very little useful information but during which extensive evolution must have occurred in the larval as well as the adult characters of these animals. As noted earlier (Orton, 1953), the major characters that differentiate the Salientia from all other known amphibians, fossil and living, are features that have fundamental effects on the structural plan in both larval and adult stages, notably the drastically altered proportions and peculiar adjustments to internal space limits associated with the excessively shortened vertebral column. It seems highly probable that a block of characters with such far-reaching effects as these must have been established through coordinated evo-

lutionary changes that modified the whole ontogeny as a unit. It is unlikely that such a sharply different structural plan could be produced by discordant changes that brought one developmental stage to the salientian level without simultaneously remodelling the other stage. The genetic changes that installed the frogs as a distinctive group were certainly attained long ago, but the early part of that history is still very inadequately known. All of the known Recent frogs and all of the well-preserved fossil frogs have essentially the same peculiar structural plan, and presumably they represent a sampling of the evolutionary lines that have branched off since the frog stock first became genetically isolated. *Protobatrachus,* of the Upper Triassic, has generally been considered a very primitive frog or a near-predecessor of the typical frogs, but recently Griffiths (1956) has interpreted the single known specimen as a partly metamorphosed tadpole, an illuminating idea which can account for virtually all of the peculiarities of the specimen and which—if correct—implies that the tadpole-frog structural plan was probably already well established by Upper Triassic times.

Cope (1889) essentially predicted the modern view of the evolutionary significance of the tadpole when he suggested: "The larval life of the Salientia has probably undergone important modifications during the course of geologic time . . . these peculiarities of larval life . . . have been gradually assumed by the larvae of the Salientia in the course of their existence, as though they were adult animals, and probably in obedience to the same kind of laws." This suggestion, which differed from the interpretation of specialized larval stages which prevailed in his time, was an obscure detail buried in his vast amount of published work, hence it is scarcely surprising that it was not followed up and that tadpole evolution received little further serious attention until G. K. Noble began his life-history studies in the 1920's.

Noble made many important contributions to frog systematics, both from his own studies and from skilled appraisal of the work of others. His most original interpretive work began when he noted that revisions based on adult characters regrouped some frogs that not only had important adult characters in common but also shared an unusual type of life history or a distinctive larval character. He followed up this clue to life-history evolution by investigating the status of frogs that shared similar life-history specializations but were supposedly unrelated, and analyzing supposed related groups which included forms with discordant life-history patterns. From this co-ordinated survey of life-history and taxonomic problems (in salamanders as well as in frogs) he concluded that the nature of the life history, including the larval characters, is an important indicator of evolutionary relationships among the amphibians.

Evolution of Developmental Characters

There is well substantiated experimental evidence from both vertebrates and invertebrates that certain developmental characters have a genetic basis. One can extrapolate from the limited known genetic evidence, and from the much more extensive observational studies on many kinds of larvae, and infer that the developmental process in general is under genetic control and hence is subject to genetic evolutionary changes. If larval and other growth characteristics had no such basis, the developmental resemblances and differences between species would be entirely random, and it would not be possible to recognize and define higher group catgeories on the basis of developmental characters. Keys to the larvae of genera (e.g., Orton, 1952) or of other group categories could not be written. That species groups can be recognized and defined in early developmental stages and that they coincide well with categories defined on adult characters implies that these developmental features do have a genetic basis and also that they have had sufficient genetic stability

through time to be retained as a common heritage by a group of diverging descendent species. Although there is much evidence to support this working hypothesis, the adoption of developmental studies as a regular working tool in the systematics of the lower vertebrates is still very slow, as one can note from almost any recent taxonomic paper on fishes or amphibians. Conspicuous advances in the use of larval and other developmental characters in systematics have been made chiefly by students of such groups as parasitic worms and certain insects in which the larval stages are economically or medically important. These cases amply show that early stages provide good taxonomic material, and that much can be accomplished in their study when there is sufficient incentive. The general lag in interest probably traces back to the persistent older practice of "granting" taxonomic value only to the characters of the mature adult (preferably the male in breeding plumage, or equivalent), and disregarding all else. It should be obvious, however, that the nature of evolutionary change in any morphological character can be determined more accurately when the whole ontogeny of that characteristic is well understood.

Since the origin of the frogs marked a fundamental departure in both larval and adult structure from all other known amphibian stocks, it should be glaringly obvious that the evolution of this group offers far more challenging problems when it is studied from the broader viewpoint of developmental systematics, utilizing evidence from the whole ontogeny. The key to successful integration of larval characters into the frog classification lies in deciphering the main patterns of tadpole evolution and determining which patterns are of basic importance and which are secondary in the broad phylogenetic sense. With some understanding of these trends, one can then apply larval data most effectively to help solve particular problems, and in addition can more easily view the origin and history of the tadpole as a part of the broader problem of vertebrate larval evolution as a whole.

Variations and specializations in tadpoles follow very orderly and definable patterns of evolution, with both conservative basic characters that help to delimit major taxonomic groups, and an elaborate network of secondary adaptive trends that cut across taxonomic lines (Orton, 1953, and unpublished data). Larval adaptive radiation and convergent adaptation have produced an abundance of modifications for pond life, stream life, arboreal life, terrestrial life (direct development), for surface feeding, and for predatory habits, and other specializations of less obvious ecological significance. These adaptive modifications are not always sharply defined morphologically, for there are many intermediates, and they have evolved repeatedly in unrelated groups throughout the order. Although such plastic adaptive trends as these are of secondary importance to the main lines of frog phylogeny, they must be worked out and understood in order to clarify the more conservative basic larval history. The combination of independent secondary trends superimposed on (and often obscuring) stable phylogenetic lines is a familiar pattern of animal evolution. It is not surprising that tadpoles follow such standard evolutionary procedures; indeed, it would be most surprising if they did not do so.

Primitive Tadpoles and Primitive Frogs

Much of the disagreement at the family level of frog classification stems from the general difficulty of discerning criteria of primitiveness and advancement within any group that is very highly specialized and presumably long isolated from all known related stocks, and yet has an uninformative fossil record. All of the known frogs are so specialized in their entire structure that characters which ordinarily help us to judge primitiveness or advancement in the amphibians as a whole are obscured, and it is difficult to find anything of clearly primitive nature in any of the frogs. Hence, in this group

there is a particular need to explore all possible clues throughout the entire life cycle, because valid evidence of relationship is not confined to any single developmental stage.

The suborder and family arrangement of the frogs proposed by Noble (1931) represented a major advancement in knowledge of this difficult group, and it has been widely adopted. Parker, Davis, and others have since made important improvements in certain sections of the classification, but Noble's conclusions still dominate most discussions of frog systematics. Studies on morphology and evolutionary trends in the tadpole stage (Orton, 1953 and unpublished data) have suggested a taxonomic grouping and phylogenetic organization that differ sharply from Noble's interpretation. Consideration of larval and adult characters together suggests a classification of the frogs into four basic groups of families, each group possessing a distinctive type of tadpole (see Orton, 1953, fig. 6). These four groups do not coincide with Noble's five suborders, but the latter have gradually lost validity with the increasing number of known exceptions to the characters on which they were based. On present knowledge, I consider a formal category of suborder in the Salientia to be both unnecessary and undesirable. In such small taxonomic groups as this, it is generally best to avoid excessive use of the supplementary named categories, in order to permit greater flexibility as knowledge advances and to avoid pedantic clutter.

The four definable larval types in the extant frogs are so stable, regardless of specific secondary specializations, that their real long-term phylogenetic significance appears virtually certain. It seems probable that the four groups of families which they help to characterize represent four major branches of salientian evolution that have been separate for a very long time. They probably do not represent all of the significant lines that have branched off during the long history of the Salientia, but simply lines that have survived. Larval characters thus suggest the way to an apparently more natural grouping of the frogs and to a better understanding of their main phylogenetic trends. In the suggested arrangement into four groups of families, I consider the Ascaphidae, Discoglossidae, and Pipidae to be comparatively primitive, as did Noble, but differ greatly from him in the interpretation of these families and in moving the Rhinophrynidae and Microhylidae to the primitive end of the scale.

The first of the four proposed groups contains the Pipidae and Rhinophrynidae. The known larval and adult characters together suggest that these are probably the most primitive Recent frogs. It would be difficult to find two series of frogs that contrast more sharply in general appearance in the adult stage than do these two families. The Pipidae are the most specialized aquatic frogs known, and *Rhinophrynus* is probably the most specialized of all known burrowing frogs. The Pipidae have long been placed at or near the primitive end of the scale, but the status of *Rhinophrynus* was long in doubt. Early authors treated it variously as a bufonid or leptodactylid, or as a monotypic family of uncertain relationships. Noble placed it in a monotypic subfamily of his very inclusive Bufonidae. The Zoological Record for 1953 still included it in the Bufonidae. Walker (1938), however, showed definitely that *Rhinophrynus* is not related to the bufonids or to the leptodactylids and that its primitive characters together with its many peculiar specializations isolate it well and fully justify its separation as a monotypic family. The tadpole of *Rhinophrynus* agrees very strikingly with those of the Pipidae, which are widely and completely separated from all other known tadpoles by the structure of the mouthparts, by the paired instead of single spiracle, and by other characters. Developmental characters of the African genus *Xenopus* and of the South American genus *Pipa* (including *Protopipa* and *Hemipipa*) are well known, but tadpoles of the other African genera, *Hymeno-*

chirus and *Pseudhymenochirus,* have apparently not yet been reported. The adult of at least one of these incompletely known forms, *Hymenochirus boettgeri,* has wide labial folds along the jaws, perhaps derived from conspicuous labial folds of the still unknown tadpole. From current knowledge of larval and adult characters it is postulated that the Rhinophrynidae are most closely related to the Pipidae; that these two families are endforms of a very ancient adaptive radiation which represents the oldest known surviving level of frog evolution; that their phylogenetic line split off at a very primitive level before the more advanced tadpole characters had evolved; and that they retain some larval characters probably very close to the ancestral basic type in the earliest true frogs. Although it may seem startling to bracket together such extreme adaptive opposites as the adult pipids and rhinophrynids, it should be noted that their suggested ancient origin would give their phylogenetic line a very long history (probably going far back into the Jurassic) with ample time to undergo an elaborate adaptive radiation with an extreme range of types, and ample time for extinction to eliminate most of them, leaving a wide gap between the known survivors.

The second basic group contains the Microhylidae. This relatively large and predominantly tropical family presents many interesting problems. The microhylids are extremely specialized, chiefly for burrowing, and their relationships both among themselves and to other frogs are difficult to interpret. Noble considered the microhylids to be a very advanced family derived from the Ranidae, and accordingly he placed them at the upper end of his classification. Parker (1934), however, found that the evidence does not indicate ranid ancestry for the microhylids, and he suggested that they are probably a much older stock than the ranids. This view is well supported by the larval characters. The single midventral spiracle of the microhylid tadpole, the distinctive pattern of mouthparts and other characters, together with the nature of the evolutionary trends (compared with characteristics and trends of tadpoles as a whole) strongly suggest a relatively primitive phylogenetic position for the microhylids. Differences from the type of tadpole that characterizes the higher families (Bufonidae, Ranidae, etc.) are of such nature that derivation of the microhylid tadpole from any stock in that group, ranid or otherwise, seems highly unlikely. The microhylid larval jaw structure most nearly resembles the pipid type, but is more complicated and shows a different pattern of evolutionary trends. The large number of forms and wide distribution of the Microhylidae give us a good opportunity to determine the stability of its peculiar type of tadpole under various ecological conditions. Microhylid tadpoles display an interesting range of specializations, in part associated with differences in feeding habits, unusual ecological adaptations, and direct development. So far as known, however, these differences are all variations of the single basic structural plan, and this stable larval type occurs throughout the Microhylidae and is restricted to this family. On present knowledge it seems probable that the microhylids originated at a comparatively primitive level in salientian history and have long been completely separate from other frogs, and that they are a terminal group which has not given rise to any of the known higher and more modern stocks.

The status of the genus *Phrynomerus* is uncertain. Parker (1934) excluded it from the Microhylidae, giving it monotypic family rank largely because it possesses intercalary cartilages. The tadpole attributed to *Phrynomerus* in the literature is a typical microhylid, and more recent authors have tended to return this genus to the Microhylidae. More extensive information on both its development and its adult anatomy would be very desirable.

The third apparently natural group of frogs comprises the Ascaphidae and Discoglossidae. On the basis of vertebral structure and other adult characters, No-

ble regarded the Ascaphidae (his Liopelmidae) as the most primitive known frogs, and designated the suborder Amphicoela for this single family. This opinion and rank designation have been widely adopted in the general zoological literature. In known larval characters, however, *Ascaphus* is essentially a discoglossid. The tadpole of *Ascaphus* is highly modified for life in swift streams, but its basic characters are those of the discoglossids and its specializations modify typical discoglossid features. These characters include a single median spiracle as in the microhylids and complex mouthparts similar in many respects to those of the higher group of families. The important recent work by the Stephensons on the direct development and adult anatomy of *Leiopelma* provides long-needed material for comparative study and should help to clarify the relationships of this genus. The development of the Philippine discoglossid, *Barbourula,* is apparently still unknown. The early fossil histories of both the discoglossid-ascaphid and the microhylid lines are apparently unknown, but these two groups probably branched off separately and are not directly related to each other. In larval characters, certainly, they have evolved along quite different lines. Their puzzling combinations of larval characters provide one of the reasons for thinking that not all of the major branches of frog evolution, particularly at the more primitive levels, have survived to Recent times.

The five families of frogs that are considered here to be the most primitive of the extant forms thus fall into three well-defined groups, and each group is characterized by a distinctive larval type. All other frogs, so far as their classification is currently understood, comprise one large group that is characterized throughout by one basic larval type, the well-known "standard polliwog" with horny mouthparts and sinistral spiracle. In this largest major section of the classification the abundant life-history material shows that the basic internal and external characters remain stable under the very wide range of known adaptive specializations which more or less drastically modify the general appearance of the tadpole. The only known forms in which basic characters are obscured are some of those with direct development (notably, *Eleutherodactylus* spp.), in which suppression of larval characters has gone to an extreme and some of the diagnostic structures simply fail to develop at all. The higher families offer many interesting problems in larval evolution and many points of disagreement and uncertainty in classification, but time limitations prevent their discussion here.

The temptation to generalize widely from thin lines of evidence is a well-known hazard in evolutionary research, and is a special problem in studies on the frogs because of the traditional reluctance of vertebrate taxonomists to rely on unfamiliar developmental data. Since the suggested re-grouping of frog families departs sharply from the widely-used Noble classification, the interpretation of larval characters and their validity in systematics may be questioned. A more conservative taxonomist may favor the idea that some or all of the presumed basic larval characters might have resulted from secondary convergent adaptations rather than from stable phylogenetic events. However, the extensive comparative study of tadpoles on which this work is based has shown clearly that the characters in question have remained stable under the impact of taxonomic diversification, extreme adaptive modification, and geographic dispersal which tadpoles (and, of course, the Salientia as a group) have obviously undergone. The apparent integrity of the four larval types and their apparent reliability as indicators of basic evolutionary lines are inferred from their restriction to, and constancy within, the particular taxonomic group which each larval type characterizes. Regardless of how specialized the known tadpoles have become in their ecological adjustments (including their feeding adaptations), they do not escape from the basic structure of their group. On present knowl-

edge the reality of these larval group characters seems beyond question, but of course the use to which they are put in tracing phylogenetic details may reflect differences of interpretation now, and it is well recognized that future discoveries may necessitate changes.

The suggestion that the very specialized pipids and rhinophrynids probably represent a more ancient stock than does *Ascaphus* poses an interesting problem in the interpretation of taxonomic characters. Primitiveness implies both relatively ancient origin and possession of relatively ancient characters, but in an incomplete record (either geologically or morphologically) these two attributes do not always appear to coincide precisely in any known species. A Recent species that is extremely primitive in the sense of coming from a very ancient stock may be so specialized in its adult characters that it has lost most of the obvious primitive features of its group. In contrast, a different Recent form that derives from a somewhat less ancient stock may have kept a more generalized adult structural plan with fewer losses of ostensibly primitive characters through secondary specializations, and may thereby wear the most obvious "primitive look" among its contemporaries. Relationships may be obscure or seem contradictory if judgement is based on too narrow a segment of the obtainable evidence, hence the importance of coordinated study of the whole animal through its whole ontogeny should be obvious. Present knowledge suggests that the Pipidae and Rhinophrynidae derive from a very ancient salientian stock and retain some very stable archaic larval characters in common, although adaptive evolution has taken these families into conspicuously opposite extremes of adult specialization. The available evidence further suggests that the relatively more advanced status of the discoglossid-ascaphid group is obscured largely because their more generalized adult format retains more features that fit our idea of what a primitive frog ought to look like.

Supplementary Evidence from the Fishes

Tadpole studies are no exception to the general rule that any research can benefit from consideration within a wider framework. There is much to be learned by treating tadpole evolution as a part of the broader problem of developmental evolution in the lower vertebrates as a whole. For example, comparative study of phylogenetic trends in jaw modifications in fishes (both skeletal and soft parts) can be very instructive in the analysis of comparable problems in tadpole history, for there are some remarkable similarities in morphological adjustments in the jaw region between tadpoles and certain fishes. Study of the external mouthparts of many kinds of tadpoles and the labial structures of salamander larvae and of certain kinds of fishes reveals convincing evidence that the lips of tadpoles are morphologically derivable from the simple labial folds that are common throughout these groups. The larvae of flyingfishes (Exocoetidae) have complex lip and barbel structures that yield important taxonomic clues comparable to the sort of information obtainable from tadpole mouthparts. Many adult fishes, especially among the Ostariophysi, have complex labial specializations which bear a striking superficial resemblance to certain kinds of lip modifications of tadpoles, as noted by Annandale and Hora (1922). Internal anatomy also reveals some notable structural analogies between tadpoles and certain fishes. In certain of the fish skulls described by Gregory (1933), most conspicuously in the catfish *Plecostomus commersoni*, the jaw pattern more or less closely suggests the condition in a typical ranid-type tadpole, particularly in the forward inclination of the quadrate, the contours of the shortened and displaced jaws, and the small mouth. It is noteworthy that modifications may follow similar designs in both vertebrate classes, and that such modifications may evolve either as temporary larval characters (in tadpoles, larval flyingfishes, etc.) or as permanent adult characters (in certain

fishes). The occurrence of analogous jaw patterns in tadpoles and certain fishes strongly suggests that a thorough comparative study of developmental stages, with emphasis on basic principles, would materially advance our understanding of the morphogenetic background of evolution in both groups. The richer evolutionary diversity of the fishes may supply more easily analyzed evidence than can be obtained from the frogs on such problems as the extent of convergence in adaptive structural modifications of the mouthparts at different phylogenetic levels, and the extent to which secondary changes in specializations may be confused with primitive simplicity. For example, present knowledge of Recent tadpole anatomy is inadequate to demonstrate unequivocally whether the possession of certain similar lip and jaw characters by tadpoles of both the discoglossid-ascaphid and the ranid types stems from a remote common ancestral stock that had attained this general level of buccal complexity, or whether these similar jaw patterns originated independently in the two groups from less complex ancestral mouthparts. Since the likelihood of solving this problem directly from fossil discoveries of such delicate tadpole structures is remote, the best approximation will be achieved indirectly from extensive comparative study of the trends in modification of the labial folds and jaw patterns that are evident throughout the extant amphibians and fishes.

Summary

To summarize: evolutionary processes can modify any characteristic that is genetically regulated, whether this be manifested in structure, function, or development, and since these attributes are unified in the life of the animal their evolution is best treated as a unified problem. The origin of the tadpole and its subsequent history form an integral part of the evolutionary history of the frogs. Coordinated study of the larval and adult characters suggests a way toward a more natural grouping of the families of frogs and a better understanding of their main lines of evolution. The likelihood that further improvements in frog classification will depend significantly on comparative study of the evolution of jaw mechanisms and labial specializations in fishes is but one example of the unexpected and interwoven trails one must be prepared to follow in systematics.

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GRACE L. ORTON, Scripps Institution of Oceanography, University of California, La Jolla, California. The work reported here is derived in part from the author's doctoral studies, conducted at the University of Michigan under the direction of Dr. Norman Hartweg. The present manuscript is somewhat modified from the paper as read. Contribution from Scripps Institution of Oceanography, New Series, No. 922

Evolutionary Developments in the Leafhoppers, the Insect Family Cicadellidae

HERBERT H. ROSS

ONE of the least appreciated yet most remarkable facts in the living world is the great number of insect species, genera, and families which exist today. This number is usually considered a sort of freak phenomenon, as if it had no real connection with the natural laws affecting other organisms, or perhaps was to be attributed to some overstimulation of the descriptive powers of insect taxonomists. Actually the tremendous number of kinds of insects is simply an expression of the continuous speciation which has occurred in insects, combined with the survival of an unusually high percentage of the total number of phyletic lines produced.

As a result of this survival we find preserved in living species of many insect groups an array of different steps in the evolution of specialized morphological conditions which permits us to reconstruct the course of evolution with considerable confidence. This is not the case in every family or genus of insects. In certain cases either survival rate of phyletic lines has been low, or our collecting has as yet unearthed only a few dissimilar types. In many large families or genera, however, we have sufficient primitive species and annectant types to form a remarkably cohesive picture of evolutionary events.

In such an analysis it is necessary to establish which are the specialized groups and which the primitive, and to ascertain finally what assemblage of primitive characters was possessed by the ancestral form of the category in question. If one is studying a certain family, information only from within that family may not give an answer to these questions. Suppose, for example, one finds a spine series ranging from a large, heavy spine, through a small, slender one, to complete absence of a spine. How can one know the direction which evolution took? Did this line start out with a big spine which became smaller and finally atrophied; with no spine, then gain a small one which subsequently increased in size; or with a medium-sized spine which became larger in one line and atrophied in another? Two lines of evidence may be brought to bear on this problem. In one approach, examination of closely related families may indicate what condition is ancestral to the assemblage of families involved. In the other approach, examination within the family may show that the spine series parallels changes in some other character for which the primitive condition is well known, allowing through this correlation the probable determination of the primitive condition of the spine character. In this latter case, when we say that the primitive condition is "well known" we tacitly imply that we are drawing on studies from groups other than the family under scrutiny, hence in reality both lines of evidence owe their value to knowledge from outside the family.

It is also true that as more characters are used in a phylogenetic analysis, the more detail can be embodied in the family tree. It has not been unusual, at least among the insects, for one character to remain virtually unchanged while another evolved at a rapid rate. Thus many branchings of the tree might occur for which no tell-tale changes would be shown by the first character. In the insects this

circumstance has led to much revision of family trees when characters from immature stages such as the larvae have been integrated with those in the adults.

This changing of family trees has led to much confusion in the minds of some students, who ask, "How can there be two family trees to the same group?" The answer is, of course, that there can't, the better substantiated one taking precedence over others. The real confusion resides in a lack of understanding of what we imply, or should imply, in a family tree.

If we accept organic evolution as a fact, then there is a true, correct family tree for every group, and that tree is the course followed by the species of the group as they evolved. It might have been by dichotomies, polychotomies, or by fenestrate recombinations of lines. The total characters of all known units of the group, fossil or living, morphological or physiological, comprise the data from which we can attempt to reconstruct the evolutionary course traversed by the organisms. Our attempts in this endeavor result in a family tree which represents the best judgment we can make on the basis of the facts we have noticed. This tentative tree is in reality a hypothesis which may or may not be correct. Each grouping and branching is a minor hypothesis which must be tested again and again as new information or deeper insight open up avenues of speculation or investigation. Our hope is to depict finally the true course of evolution.

An interesting example which embodies many of these problems is afforded by some studies undertaken in the leafhoppers. The problem started as an attempt to diagram the phylogeny of a single genus, *Erythroneura*. To verify the primitive nature of certain characters found in supposedly primitive species of the genus it was necessary to study the phylogeny of the sub-family to which *Erythroneura* belonged, and this in turn led inexorably to an attempt to find out the relationships of the entire family.

The Family Cicadellidae

The leafhoppers, the family Cicadellidae, comprise one of the truly large families of insects. Over a thousand genera and approximately 15,000 species have been described from the world. Although the great bulk of these are surprisingly uniform in appearance, many are bizarre forms. Some of the latter have horns, ridges, or projections on head or thorax; some are long, slender, and flattened; and others are short and squat. Certain odd shapes, especially elongate types, have arisen independently in many phyletic lines, with the result that totally unrelated genera may superficially resemble one another to a startling and completely misleading degree. This combination of convergence in some genera and widespread basic similarity in others, coupled with the unwieldy size of the group, has contributed to a confused understanding of relationships within the family.

The Cicadellidae belong to the order Hemiptera, suborder Homoptera, and are most closely related to the tree hoppers or Membracidae. These latter are characterized chiefly by an enlargement of the pronotum into a median crest or a more complicated structure (Fig. 1, *left*). In the leafhoppers the pronotum is usually wide and flat (Fig. 1, *right*) with at most a low median crest. A number of aberrant genera of leafhoppers have been segregated by recent authors (Evans, 1946) into three families, the Aetalionidae, Hylicidae, and Eurymelidae, all three supposedly intermediate between the Cicadellidae and Membracidae. The family Cercopidae, comprising the spittle bugs, is also a close relative of the Cicadellidae-Membracidae complex although distinct on the basis of many characters.

At the suggestion of my colleague, Dr. M. W. Sanderson, who uses the method in his studies of beetles, I cleared the bodies of sample leafhoppers in KOH solution to remove muscles and viscera. In treating dark species an aqueous solution of hydro-

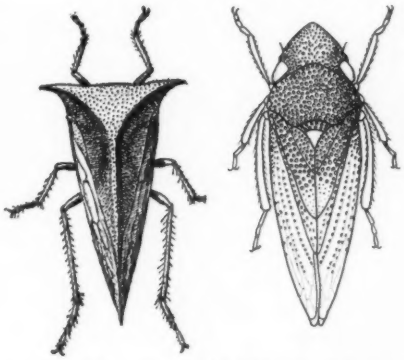

FIG. 1. *Left,* a membracid of the genus *Ceresa;* the pronotum covers the entire dorsum of the insect except for the wings. *Right,* a cicadellid of the genus *Xerophloea;* the pronotum is the large sclerite between the head and the bases of the wings. (Courtesy of Kansas State College and Illinois Natural History Survey.)

gen peroxide and ammonia proved highly satisfactory to bleach out some of the dark integumental pigments. In these treated specimens details could be seen of many skeletal structures not visible in uncleared specimens.

After completing a survey of representatives of each of all six families and most of the subfamilies and tribes of Cicadellidae, hitherto unused characters were noticed in some dorsal and ventral plates of the thorax, especially the mesonotum and metanotum and the ventral area called the mesosternum. Both the tibia and femur of the hind legs proved to have characters of importance. There follows a brief summary of these and other structures useful in the induction of a phylogenetic tree (Fig. 4).

Mesosternum. This plate is separated from the side plates or pleurae in the Cercopidae and all but one aberrant subfamily of Cicadellidae by a well-marked sternopleural suture (Fig. 2, *C, E*). In the Membracidae this suture is obliterated. In all the families the mesosternum has a median sternal suture marking the lines of origin of internal struts or thickenings. This sternal suture is Y-shaped in the Cercopidae, Membracidae, and all but two subfamilies of Cicadellidae. In these two subfamilies, the Ulopinae and Cicadellinae, the two arms of the Y arise almost directly from the posterior margin of the segment. This distribution of characters indicates that a Y-shaped sternal suture and distinct sternopleural sutures are primitive characters in this group of families.

Mesonotum. In the Cicadellidae and Cercopidae and some of the less ornate Membracidae an anterior triangular area, the praescutum, is defined by sutures or indicated by furrows (Fig. 2,*H*). In the Cicadellidae the scutum (the area posterior to the praescutum) has an indistinct transverse groove or valley; in the Cercopidae this groove is not defined. Judged by conditions in other Homoptera, the condition of both praescutum and scutum found in the Cercopidae is the primitive one. In the Membracidae a remarkable change has occurred. The indistinct scutal grooves of the leafhoppers have become distinct sutures, the transcutal sutures, marking the course of a new internal ridge (Fig. 2,*I*).

Metanotum. In the Cercopidae, some Cicadellidae, and many Membracidae the metanotum has a median suture usually associated with an internal flange (Fig. 2,*F*). In many Cicadellidae this median suture and flange are absent. The evidence is conclusive that the suture is a primitive one which has atrophied in several phyletic lines.

Head. Two head structures are of interest here. In the Membracidae, Cercopidae, and a few Cicadellidae the epicranial arms and stem form an inverted Y. This is the usual insectan structure and is undoubtedly the primitive condition in the leafhoppers. In most Cicadellidae the junction of arms and stem is obliterated and the arms are either differently situated or have become partially atrophied. The epistomal suture, another primitive insectan feature, is present in the Membracidae and Cercopidae, but it is either

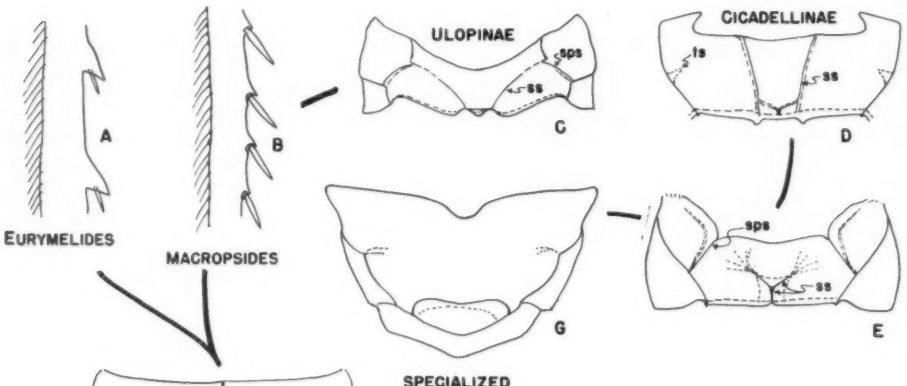

FIG. 2. Thoracic structures of Cicadellidae (*A–H*) and Membracidae (*I*). *A*, portion of hind tibia of *Stenocotis; B*, same of *Macropsis; C*, mesosternum of *Moonia; D*, same of *Empoasca; E*, same of *Paraphlepsius; F*, metanotum of *Macropsis; G*, same of *Balclutha; H*, mesonotum of *Macropsis; I*, same of *Aetalion; ms*, median metanotal suture; *pas*, parascutal sutures; *ps*, praescutal suture or furrow; *sps*, sternopleural suture; *ss*, median sternal suture;*ts*, trace of sternopleural suture. Arrangement indicates major branches of cicadellid phylogeny.

lost or its identity is extremely doubtful in the Cicadellidae.

Hind leg, tibia. The Cicadellidae may be divided into two groups on the basis of characteristics of the hind tibia. In one group the tibia has a lateral row of large spines, each with a macroseta or hair set in it (Fig. 2,*A*). In the other the tibia has a regular lateral row of large macrosetae, each set in a large basal socket (Fig. 2,*B*). In the Membracidae the tibia is simpler, having only ordinary hair or small setae laterally. In the Cercopidae the tibia has two or three large lateral spines resembling but not exactly like those found in the first group of the Cicadellidae.

Hind leg, femur. The apex of the femur is unadorned in both the Cercopidae and Membracidae, but in the Cicadellidae bears from two to five macrosetae (Fig. 3). The numbers of these macrosetae were used effectively by Ribault (1952) in his keys to the leafhoppers of France. Intensive scrutiny has shown that the relative position of these macrosetae is remarkably similar throughout many groups, although the assemblage of macrosetae as a whole may be at the apex of the femur or in a more basal position.

Membracidae vs. *Cicadellidae*

Our main problem in this section is to apply the preceding information to an evaluation of the relationships of the

Membracidae, Cicadellidae, and the three families supposedly intermediate between them. In this discussion it will frequently be profitable to refer to the distinctive but closely related family Cercopidae, in which many characters are more primitive than those of the complex under study.

In comparing the Membracidae and Cicadellidae the following salient points appear. The Membracidae have undergone two specializations which have not occurred in the Cicadellidae: the evolution of a transcutal suture and the loss of the sternopleural sutures. The Cicadellidae have undergone three specializations which have not occurred in the Membracidae: the loss of the epistomal suture, the development of lateral macrosetae or spines on the hind tibia, and the addition of a set of macrosetae on the hind femur. It follows that neither family could have arisen from the other, but that they must have evolved from a common ancestor in which all five of these characters were primitive, as follows: epistomal suture present, sternopleural suture present, scutum probably with faint grooves but no transverse suture, hind femur without apical macrosetae, and hind tibia without lateral macrosetae or spines. It is interesting that all of these except the last are found in the Cercopidae. Examining the three intermediate families, we find that the Aetalionidae have all the characters listed for the Membracidae, even to having the pronotum markedly enlarged in comparison with that of the Cicadellidae; and both the Hylicidae and Eurymelidae have all the characters listed above for the Cicadellidae.

It seems logical, therefore, to consider *Aetalion* and its allies as a primitive subfamily (Aetalioninae) of the Membracidae, and to transfer the Hylicidae and Eurymelidae back to the Cicadellidae.

For the Membracidae we can deduce an interesting picture. From the membracidcicadellid ancestor the family arose as a branch in which the pronotum enlarged and simultaneously the sternal and pleural regions of the mesonotum fused and an additional internal strut evolved under the mesonotum. Perhaps the mesothoracic changes provided a stronger foundation for the wings in propelling the resultant more bulky insect in flight. The first known stage in membracid evolution is represented by the Aetalioninae, in which the praescutum is still well indicated. In succeeding stages all traces of the praescutum were lost and the pronotum became larger. Ultimately the pronotum evolved into a huge structure dwarfing the mesonotum and metanotum, whose structure became further modified. The subfamily Centrotinae represents a surviving intermediate stage in the series, the Membracinae an advance one.

Evolution within the Cicadellidae

Returning to the Cicadellidae, there seem to be few sustained evolutionary trends like those noted in the Membracidae. Certain primitive characters, however, mark a few genera or groups of genera as early offshoots of the cicadelline stem. Thus the median mesonotal suture (Fig. 2,*F*) occurs in the subfamilies Idiocerinae, Macropsinae, and Eurymelinae, and in some genera of the Ledrinae and Tartessinae. The epicranial arms occupy a primitive inverted-V position in some genera of the Eurymelinae and Agalliinae. These subfamilies must represent early phyletic branches which became differentiated before these two primitive characters were lost.

Turning to an examination of leg structures, it is at once apparent that two sets of characters offer possibilities for defining specialized segregates of genera and subfamilies. In one segregate, comprising the Eurymelinae, Hylicinae, and Ledrinae, the hind tibia possesses a row of large spines each bearing a macroseta (Fig. 2, *A*), whereas in all other leafhoppers the lateral edge bears only a row of macrosetae (Fig. 2,*B*). If we examine all sides of the leafhopper tibia we find that in all groups either two or three additional

edges bear rows of macrosetae much like those in Figure 2,*B*. It seems reasonable to suppose that this is the primitive condition for all rows of tibial spurs, and that the spined condition is a specialization. In the three subfamilies having this spined condition the apical macrosetae of the hind femur are uniformly small and, compared with the condition in other subfamilies, spaced relatively far apart. On the basis of both characters, the Eurymelinae, Hylicinae, and Ledrinae appear to be a monophyletic leafhopper branch which I am calling the division Eurymelides. Within the Eurymelides certain genera such as *Eurymela* and *Stenocotis* possess the median metanotal suture, and *Eurymela* has a primitive condition of the epicranial arms. The occurrence of these archaic characters means that the division Eurymelides arose from an early point on the leafhopper family tree.

The division Eurymelides is, with few exceptions, confined to the Old World, and contains many diverse and bizarre genera. In some of them, for example *Ledra* and *Wolfiella*, the median metanotal suture is nearly or completely obliterated, but these genera appear to be only distant relatives. The metanotal suture has therefore disappeared independently in at least two separate phyletic lines within the Eurymelides. This division needs more study before the phylogeny of its components can be charted.

The second set of distinctive leg structures comprises the macrosetae at the apex of the hind femur. In most members of the division Eurymelides and in certain primitive subfamilies such as the Macropsinae and Agalliinae, the hind femur has only three macrosetae, *a* and *b* apical and *c* preapical and lateral (Fig. 3,*A*). In many other subfamilies, however, these macrosetae number five (*a–e*), arranged as follows: *a* and *b* are a pair at or closest to the apex; *c* and *d* are lateral, basal to *b*, and in tandem order; and *e* is situated immediately or almost so above *c* (Fig. 3,*B, D, G*). It seems highly unlikely that this precise arrangement of macrosetae would arise twice independently, hence it is logical to conclude that the subfamilies possessing the arrangement constitute a monophyletic line, here designated as the division Tartessides. In one small complex of subfamilies (the Tartessinae and Coelidiinae) the median metanotal suture is either distinct or at least faintly indicated, but in all the other subfamilies in the line this suture is completely atrophied. On the basis of this preservation of a primitive character we may conclude that the Tartessinae and Coelidiinae are the most primitive existing offshoot from the tartessidine line. In the Tartessinae and Coelidiinae also macroseta *e* occurs in a notch on the top edge of the femur, whereas in the other subfamilies macroseta *e* is situated just over the top edge on the lateral face of the femur.

Within the subfamilies having the five femoral macrosetae a well-marked evolutionary change is evident. In the primitive subfamily Tartessinae macrosetae *a* and *b* occur on the end rim of the hind femur adjacent to and almost touching the dorsal portion of the membrane connecting femur and tibia (Fig. 3,*B*). The same is true in many other subfamilies outside the tartessidine line, such as the Agalliinae, Eurymelinae, and Macropsinae. The apical position of macrosetae *a* and *b* therefore may be regarded as a primitive condition. In the Iassinae, Deltocephalinae, and Hecalinae macrosetae *a* and *b* are in a preapical position, occurring on the top side of the femur a short distance before the apex (Fig. 3,*D*) and the other three macrosetae are also correspondingly farther from the apex; in the Aphrodinae the set of macrosetae is even farther basad (Fig. 3,*G*); and in the Penthimiinae the entire set of macrosetae occurs on a preapical protuberance (Fig. 3,*I*). Thus in the tartessidine line the macrosetae started at the apex of the femur and gradually moved to positions more toward the base.

In a few subfamilies such as the Tettigellinae and Nirvaninae the hind femur

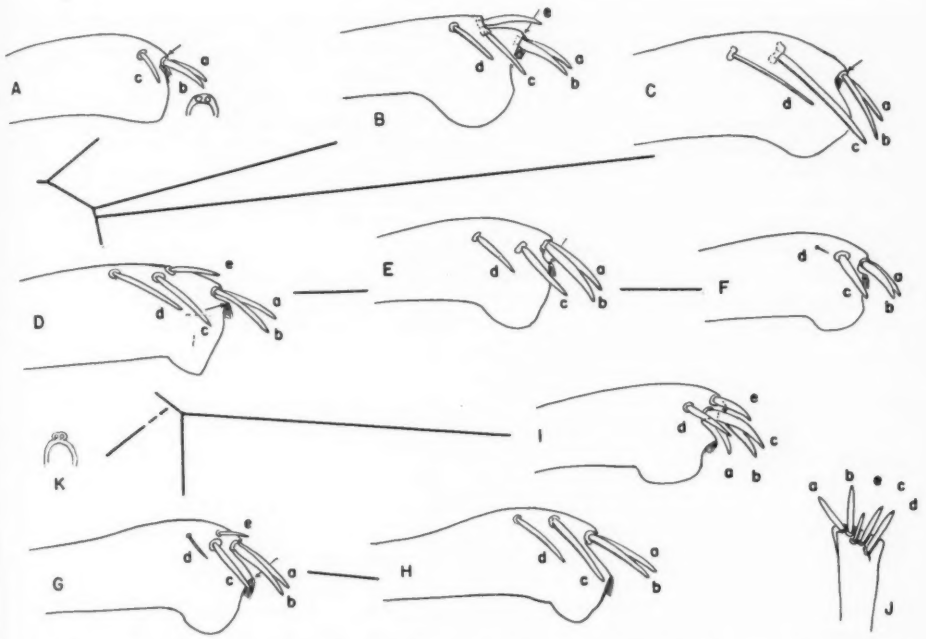

FIG. 3. Apex of hind femur of Cicadellidae, showing macrosetae *a–e*. *A, Macropsis; B, Coelidia; C, Empoasca; D, Balclutha; E, Nirvana; F, Nionia; G, Aphrodes; H, Xestocephalus; I, J, Penthimia; K, Dorycephalus. A–I,* lateral aspect; *J,* dorsal aspect; *K* and insert for *A,* end view. Arrangement indicates direction of evolutionary change. Arrows indicate end of dorsal margin of femur.

has only four macrosetae, *e* being absent. The relative position of the remaining four is exactly like that of *a, b, c,* and *d* in subfamilies possessing all five. An additional point of great interest is this: In certain of these subfamilies, e.g., Tettigellinae and Cicadellinae, macrosetae *a* and *b* are apical (Fig. 3,*C*); in the Nirvaninae and Nioniinae macrosetae *a* and *b* are preapical to the same degree as in the Iassinae (Fig. 3,*E*); and in the genus *Xestocephalus a* and *b* are even more preapical (Fig. 3,*H*), exactly as in certain Aphrodinae. These facts seem logically to fit only one explanation, namely, that each subfamily arose from an ancestor possessing all five femoral macrosetae (that is, from some point on the tartessidine line), and in each subfamily macroseta *e* dropped out independently. With only a few exceptions which will be discussed at the end of this section, this conclusion draws into one unit all the leafhoppers in which the ocelli are either in a dorsal position on the head, or on the ridge which separates the dorsal and frontal areas.

On the basis of these facts and conclusions it is possible to reconstruct the probable steps which occurred in the evolution of the tartessidine line (Fig. 4). The ancestral form possessed the metanotal suture and five macrosetae on the hind femur; the latter was in all probability unnotched with macroseta *e* situated just below the dorsal margin as in Figure 3, *D*. From this ancestor two lines arose. In one the metanotal suture persisted but macroseta *e* moved to a dorsal position and the profile of the femora became

notched at its point of attachment (Fig. 3,*B*). The subgamily Tartessinae represents such a stage; in a side branch comprising the Coelidiinae the metanotal suture became weak and finally disappeared but macroseta *e* remained in the dorsal position.

In the other tartessidine line the metanotal suture disappeared completely. No living form is known representing such a stage, but the two subfamilies Tettigellinae and Cicadellinae appear to be side branches from such an ancestor in which macroseta *e* disappeared (Fig. 3,*C*). In the mesosternum of the Cicadellinae the sternopleural sutures are atrophied and the two arms of the sternal suture form parallel lines running the full length of the sclerite (Fig. 2,*D*). In the line beyond the tettigelline-cicadelline branch, the macrosetae moved away from the apex of the femur, resulting in a condition like that found in the Deltocephalinae (Fig. 3, *D*). From this point on the tree several distinctive branches evolved. In one, resulting in the Iassinae, the epicranial arms atrophied above the antennae. In a second branch, represented by the Aphrodinae, the femoral macrosetae became more basal in position (Fig. 3,*G*). In one genus of Aphrodinae macroseta *e* atrophied (Fig. 3,*H*). The two subfamilies Nirvaninae and Nioniinae appear to be a third branch from this point in which macroseta *e* disappeared, although the two subfamilies may actually have arisen separately. In a fourth branch the ninth male sternite became triangular, in contrast to the straplike condition in other leafhoppers, and from this branch evolved the closely related subfamilies Deltocephalinae and Hecalinae. It is highly likely that the Penthimiinae arose from a fork of this latter branch in which the femoral spines became clustered on a preapical hump (Fig. 3,*I, J*), because the ninth sternite and other male structures show a striking similarity with those of certain Deltocephalinae.

The above definition of the eurymelidine line and the chief components of the tartessidine line accounts for all but a few subfamilies of leafhoppers. Of this remainder, four are noteworthy in having at least some genera with a simple, declivous head possessing only an indistinct dorsal area and having the ocelli on the face. In two subfamilies, the Macropsinae and the Idiocerinae, the primitive median metanotal sutures are present; in the other two, the Agalliinae and Ulopinae, the heads of at least their primitive genera have simple, inverted-V, epicranial sutures. Presumably all four arose from an ancestral form possessing a simple, primitive head and metanotal suture. In one line, which gave rise to the Idiocerinae and Macropsinae, only minor changes of epicranial sutures occurred, but in the other line the metanotal sutures were lost. In this latter line another branching occurred. One branch remained simple and evolved into the primitive forms of the Agalliinae. In the other branch, which evolved into the Ulopinae, the mesosternal sutures became re-aligned as in Figure 2,*C*.

Another unplaced subfamily is the Xerophloeinae which has many points of similarity with *Stenocotis* and some other primitive genera belonging to the division Eurymelides. Similarities of particular significance include the exposed proepisterna (hidden in most leafhoppers), the possession of a second row of apical tibial spines, and a number of details concerning the exact shape and arrangement of the femoral mascrosetae. The Xerophloeinae are more primitive than the Eurymelides in possessing only typical macrosetae down the lateral edge of the hind tibia. At the present moment, therefore, it appears that the Xerophloeinae arose from the extreme base of the eurymelidine line and may best be designated as a separate small division of the family, the Xerophloeides.

The three subfamilies left to be considered, the Dorycephalinae, Eupelecinae, and Koebeliinae, contain only one or two genera each, and all have a foliaceous head very like that of some Hecalinae. They

agree with this family also in the triangular male ninth sternite and wide male plates. In all three, however, the femoral spines are reduced, only *a*, *b*, and sometimes *c* being large, the others absent or minute. Within certain genera such as *Aphrodes* the femoral spines become reduced from a larger number. On the basis of this rather tenuous comparison with *Aphrodes*, and in conjunction with the other characters listed, I am tentatively considering that the Dorycephalinae, Eupelecinae, and Koebeliinae are offshoots of the hecaline stem which have undergone reduction in femoral spines.

A few described tribes have been unavailable for study but these are chiefly small, aberrant groups which, judged from descriptions in the literature, offer no evidence contrary to the general trends expressed here.

An interesting question remains concerning the macrosetae on the hind femur. Did the ancestor of our present-day leafhoppers have three or five of these macrosetae? The answer may be five, in which case the Macropsides and Xerophloeides lost two; or it may be three, in which case the extra two were added during the early evolution of the tartessidine line. From the data at hand it seems impossible to resolve this question.

Synopsis of Divisions and Nearctic Subfamilies of Cicadellidae

Because this evolutionary outline has led to the adoption of some changes in supergeneric categories, the resultant classification is here tabulated. Following the precedent of Evans I am using the category "division" for the primary phylogenetic groups of the family.

DIVISION Eurymelides. Hind tibia with several lateral spines, each with a preapical macroseta (Fig. 2,*A*); primitive genera having distinct median metanotal suture. Hind femur having short apical macrosetae *a* and *b;* in some genera *c* also is present, near the apex of the femur. Contains three chiefly tropical subfamilies, the Eurymelinae (having distinct epicranial stem and arms), Hylicinae (having a large appendix on the forewing), and Ledrinae.

DIVISION Macropsides. In this and the two following divisions the hind tibia has a lateral row of enlarged macrosetae arising from conspicuous bases. In the Macropsides the base of femoral macrosetae *a* and *b* are set in the apical edge of the hind femur. The primitive genera retain the median metanotal suture (Fig. 3, *F*). Four subfamilies are placed here, including the Old World Ulopinae (Ulopini and Cephalelini of Evans, 1947).

Macropsinae. The hind femur has macroseta *c* at or before apex (Fig. 4,*A*); the head is short, without epicranial sutures above antennae, the base of the latter beneath overhanging ledges. North American genera: *Macropsis* Lewis and *Oncopsis* Burmeister.

Idiocerinae. Hind femur lacking macroseta *c;* head short, with sutures extending dorsad to ocelli, and without ledges over antennal bases. Sole North American genus: *Idiocerus* Lewis.

Agalliinae. Median metanotal suture atrophied. Either epicranial sutures or their traces Y-shaped, the ocelli situated some distance from them, or the head warty and bearing deep, sharp folds; hind femur with only macrosetae *a*, *b*, and *c*, *a* and *b* apical as in Figure 4,*A*. Chiefly small, robust species with short head. North American tribes: Agalliini and Megophthalmini (treated as closely related subfamilies in Oman, 1949).

DIVISION Xerophloeides. Hind femur with macroseta *c;* head with flat anterior projecting portion, ocelli on dorsum and near meson; proepisterna exposed and punctate like the adjacent collar; median metanotal suture very thin and indistinct. Sole genus: *Xerophloea* Germar, subfamily Xerophloeinae.

DIVISION Tartessides. Hind femur having five macrosetae in primitive genera. The median metanotal suture is distinct only in the Tartessinae and some Coelidiinae.

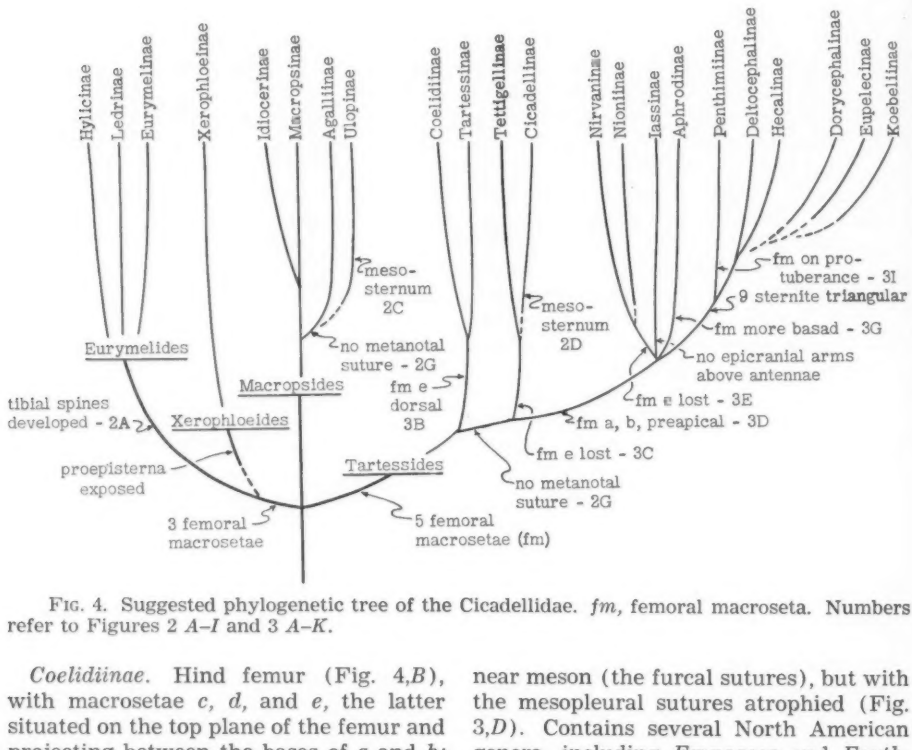

FIG. 4. Suggested phylogenetic tree of the Cicadellidae. *fm*, femoral macroseta. Numbers refer to Figures 2 *A–I* and 3 *A–K*.

Coelidiinae. Hind femur (Fig. 4,*B*), with macrosetae *c*, *d*, and *e*, the latter situated on the top plane of the femur and projecting between the bases of *a* and *b*; head with sutures reaching ocelli, and with head surface raised slightly above level of eye which therefore appears to be slightly flanged; posterior portion of praescutal furrows atrophied; mesal metanotal suture only faintly indicated and without an internal apodeme. North American tribes: Coelidiini (Jassinae of American authors prior to 1949) and Neocoelidiini. These were treated as separate subfamilies by Oman (1949).

Tettigellinae. Head with frontal area enlarged and ocelli on dorsum; hind femur with macrosetae *a* and *b* apical, *c* and an added *d* tandem and preapical, as in Figure 4,*C*. A large group here defined as in Oman (1949).

Cicadellinae. Head short but very deep, with epicranial arms extending to ocelli or their vestiges; mesosternum completely subdivided by a pair of parallel sutures near meson (the furcal sutures), but with the mesopleural sutures atrophied (Fig. 3,*D*). Contains several North American genera, including *Empoasca* and *Erythroneura*.

Nioniinae. Head short, with epicranial sutures forming circle beneath ocelli; hind femur with macrosetae *a* and *b* preapical, *c* large, and *d* minute (Fig. 4,*E*). Sole genus: *Nionia* Ball.

The next five families share a most peculiar arrangement of hind femoral macrosetae (Fig. 4,*F*): *a* and *b* are preapical, *c* and *d* usually large, and a fifth is present, *e*, situated above *c* but still on the lateral margin just below the dorsal midline of the femur.

Iassinae. Head with epicranial arms atrophied above level of antennae; hind femoral macrosetae as described above. North American tribes: Iassini (formerly Bythoscopinae) and Gyponini.

Aphrodinae. Head with epicranial arms reaching vicinity of ocelli; hind femur with macrosetal complex situated a con-

siderable distance from apex; male genitalia in this and *all following subfamilies* with triangular ninth sternite and usually with male plates wide at base. North American genera: *Aphrodes* Curtis (with all femoral macrosetae) and *Xestocephalus* Van Duzee (with femoral macroseta *c* atrophied and *e* enlarged, or *e* atrophied and *c* migrated dorsad).

Penthimiinae. A branch much like the Aphrodinae; hind femoral macrosetae situated close together on a raised knob. Sole genus: *Penthimia* Germar.

Deltocephalinae. Head with epicranial arms reaching ocelli, the latter on the anterior edge of the head; hind femur with full complement of macrosetae, *a* and *b* slightly to moderately preapical (Fig. 4, *F*). This subfamily is the largest, most diverse, and most widely distributed in the entire family Cicadellidae. The Nearctic fauna alone represents about 150 genera. It has been divided into a series of tribes by Oman (1949), and contains in addition the tribe Selenocephalini of Evans (1947). The Nearctic genus *Dorydiella* Baker very likely belongs to this latter tribe. As pointed out by DeLong (1923) the nymph of *Dorydiella* has an unusual head projection, quite unlike other Deltocephalinae, and in this respect it is similar to the nymph of the oriental selenocephaline *Drabescus* Stal (see Evans, 1947, p. 218, fig. 31).

Hecalinae. Similar to Deltocephalinae, differing chiefly in having the cheeks angularly incised under each eye. In most genera the head is produced into a long, foliaceous projection. Six genera occur in the Nearctic region.

Koebeliinae. Head with foliaceous anterior margin, ocelli on ventral side distant from eyes, and cheeks angulate below eyes; hind femur with macrosetae *a* and *b* slightly but distinctly preapical, *d* absent, *c* and *e* small, the latter (if correctly identified) dorsal. Sole genus: *Koebelia* Baker, of doubtful affinities.

Dorycephalinae. Head with elongate foliaceous anterior projection, ocelli on edge near eyes, and cheeks angulate; propleurae exposed and rectangular; hind femur with macrosetae *a* and *b* slightly preapical (Fig. 4,*K*) but other macrosetae small or atrophied. North American genera: *Dorycephalus* Kouchakewitch and *Neoslossonia* Van Duzee. This distinctive group is also of doubtful phylogenetic position.

In Summation

We now can view the evolution of the major groups of leafhoppers as a series of branchings accompanied by the development of tibial spines, loss of thoracic sutures, changes in epicranial sutures, and in the evolution of a definite number and arrangement of macrosetae on the hind femur. The groups progress logically from primitive to specialized, and each change appears as a simple derivation of its immediately ancestral condition. But this result must be regarded as only another step in a continuing study. We need to search for other characters or representatives not only to attempt to establish the phylogenetic position of the subfamilies either placed only tentatively in the present scheme or not available for study, but also to test the parts we consider well founded. We should not forget that little has been done but much could be in working out the evolution of individual subfamilies and genera of the leafhoppers.

In addition to these considerations, others arise. We presumably have now a general idea concerning what morphological steps took place in the evolution of the leafhopper groups. What steps occurred in the physiological attributes of these forms? What bearing had these on the unusual success of this extremely abundant family? Possibly the best beginning on these puzzles would be to investigate the question, How do ecological characteristics correlate with morphological characteristics and with the evolution of the different entities? Some of these questions may seem to be outside the domain of the systematist, but who

(*Concluded on p. 69*)

Points of View

Misuse of Generic Names of Shrimp (Family Penaeidae)

Misuse of names of the penaeid shrimp has been going on for well over a hundred years. The matter is of some importance because interest in these shrimp, both zoologically and commercially, is increasing greatly every year and use of the Latin names in general papers and statistical reports is increasing commensurately. Most authors are non-taxonomists and follow rather faithfully the erroneous spellings of reputedly authoritative works. Some of these spellings are wrong for the same reasons other words are sometimes spelled wrong. Others are based upon misconceptions. The latter are the more important and are the only ones treated in these remarks.

Peneus was first used as a generic name in a species list by F. Weber in 1795. The three species named were not described nor was the genus characterized, and all three species names were followed by the letter "S." In the introduction (p. III) Weber states that the "S" stands for "Supplementum insectorum ineditum Fabricii." Thus *Peneus* was a *nomen nudum* and remains one, for when Fabricius did publish his *Supplementum* in 1798, defining his genus about as well as things were done in those days, he used the word *Penaeus*. Whether or not this is the proper way to latinize a Greek name is beside the point with regard to zoological nomenclature. The genus was restricted by S. I. Smith (1886), who also used *Penaeus*. Practically all other authors have used the same name. There were some exceptions.

Lucas (1848) used *Penoeus*, with the *oe* as a ligature and, according to Burkenroad (1934), in a later publication which I have not seen, Lucas (1849) used *Peneus*. Philippi (1840) also used *Peneus*. Lucas' use of the ligature *oe* may have been a printer's error, for in many of the older fonts the *a* in the *ae* ligature was script-like and therefore easily confused with the *oe*.

Smith (1871, not 1869 as is commonly stated) used *Peneus* and in the same paper described the genus *Xiphopeneus*. Later when he realized that *Peneus* was wrong and took up Fabricius' original spelling, he recognized that *Xiphopeneus* would have to stand (Smith 1882, 1886). The doyen of American carcinologists, Waldo L. Schmitt, apparently had a similar experience, for in 1926 he used *Peneus*, citing Weber as the original authority, but turned to *Penaeus* later (Schmitt, 1926, 1935).

The papers of Smith (1871) and Alcock (1901, 1905) really laid the grounds for the present confusion. Alcock used *Peneus* throughout and in his 1905 synonymic lists did not bother to give the spellings really used by the authors; thus, this paper is useless in that respect, except for the dates, and in error. In one place Alcock did say that Fabricius' name was *Penaeus*, but that was evidently an oversight on his part. These facts would make little difference, except that Alcock described certain new genera, *Atypopeneus*, *Parapeneopsis*, and *Trachypeneus*, in conformity with his idea of how *Penaeus* should be spelled. These names plus *Xiphopeneus* of Smith and *Trachypeneopsis* of Burkenroad (1934) do not conform to eight other shrimp genera where the word *Penaeus* or the root is used. This is unfortunate, but although the International Commission has advised against giving similar but different spellings for genera in the same family, the generic names cannot be changed once they are properly published, regardless of authors'

misconceptions or other matters. This is one of the basic rules upon which nomenclatural stability rests. Nevertheless, Anderson and Lindner (1943) emulated Alcock, but in the opposite direction, and changed everything except *Trachypeneus* to conform with *Penaeus*. Since this key has been used extensively, the misspellings, *Xiphopenaeus*, etc., have become widely disseminated. There are also some unfortunate misspellings of species names in this paper, but here we are concerned only with generic names. These remarks should in nowise be taken as a criticism of the general value of Anderson and Lindner's paper, for, in spite of one minor taxonomic error, it summarizes a great deal of literature, some of which is written in a style more concealing than revealing. Therefore, it is, as one carcinologist said, "one of the most useful penaeid papers of the century."

Dr. Fenner A. Chace, Jr. has recently drawn up a list of the generic names of the Penaeidae, which he has kindly allowed me to publish here.

The Genera of Shrimps of the Family *Penaeidae*

Subfamily SOLENOCERINAE

Haliporus Bate, 1881
Hymenopenaeus Smith, 1882
Solenocera Lucas, 1849

Subfamily ARISTAEINAE

Aristaeomorpha Wood-Mason, 1891
Aristeus Duvernoy, 1840
Bentheogennema Burkenroad, 1936
Benthesicymus Bate, 1881
Gennadas Bate, 1881
Hemipenaeus Bate, 1881
Hepomadus Bate, 1881
Plesiopenaeus Bate, 1881

Subfamily PENAEINAE

Artemesia Bate, 1888
Atypopeneus Alcock, 1905
Funchalia Johnson, 1868 (including *Pelagopenaeus* Burkenroad, 1934)
Heteropenaeus De Man, 1896
Macropetasma Stebbing, 1914
Metapenaeus Wood-Mason, 1891
Parapenaeus Smith, 1885
Parapeneopsis Alcock, 1901
Penaeopsis Bate, 1881 (including *Metapenaeopsis* Bouvier, 1905)
Penaeus Fabricius, 1798
Protrachypene Burkenroad, 1934
Trachypeneopsis Burkenroad, 1934
Trachypeneus Alcock, 1901 (including *Trachysalambria* Burkenroad, 1934)
Xiphopeneus Smith, 1871

Subfamily SICYONINAE

Sicyonia H. Milne Edwards, 1830

These names are correct as written and, under the Rules, cannot be changed by authors for purposes of uniformity. It should not strain the minds of zoologists much further to remember that five genera of penaeids are spelled with *e* rather that *ae*. This seems to be preferable to applying to the International Commission for a plenary ruling bringing about uniformity, although that avenue is open.

In the first place, such action might set a precedent leading to a host of appeals over similar minutia; secondly the matter is not determinable on the basis of any clear grammatical rule, but shades off into matters of usage, preference or even original pronunciation about which we know little. The ligature *ae* was often changed to *e* in English and other European languages and such words as aesthetic, aether, etc. became esthetic, etc. However, this sets no precedent for Latin. Instead, printers have set one themselves for zoological Latin by dropping the ligature from their fonts within the past fifty years, while equating the ligature to the simple digraph *ae*. Thus, all older workers spelled *Penaeus* with the ligature, but since about 1910 the usage has almost ceased and it is now a rare printing press which has the ligature in its font.

If the matter of uniformity were settled on a basis of majority usage, the *ae* spelling would easily be selected. Fabricius (1898), Spence Bate (1881), S. I. Smith

(1882, 1885), Wood-Mason (1891) and De Man (1896) named eight genera, using *ae*. These genera probably contain the majority of species. Furthermore, Latreille, H. and A. Milne-Edwards, Heller, Bouvier and most other students of shrimp followed this spelling. In contrast, S. I. Smith (1871), Alcock (1901, 1905) and Burkenroad (1934) named five genera using the *e* spelling. (All papers in this paragraph are not cited. They can be easily traced from taxonomic papers).

The argument has been raised that *Peneus* was the proper spelling of the Latin name of a river in Thessaly and also the name of a river god. However, I can see the fortunate aspect of an error, if error it was, by which Fabricius failed to name a group of marine animals after a river or a mythical fresh-water god. Similarly, I attach little importance to the desire to rectify the matter now. Other aspects of the case are considerably more important.

Some curious inequities would arise from any plenary ruling for uniformity. If *Peneus* were adopted, among the authors listing several genera, only Alcock, whose usage was mostly wrong under the rules when he wrote, would in a sense be validated. If *Penaeus* were adopted, the only authors generally validated would be Anderson and Lindner (1943), who were in good part wrong when they wrote. Some names in most other papers including recent papers (cf. Burkenroad, 1934, 1939 and Voss, 1955, who were carefully correct) would be wrong. Injustices would be done to careful authors by any plenary ruling, and there would be no profit in it.

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GORDON GUNTER
Gulf Coast Research Laboratory
Ocean Springs, Mississippi

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